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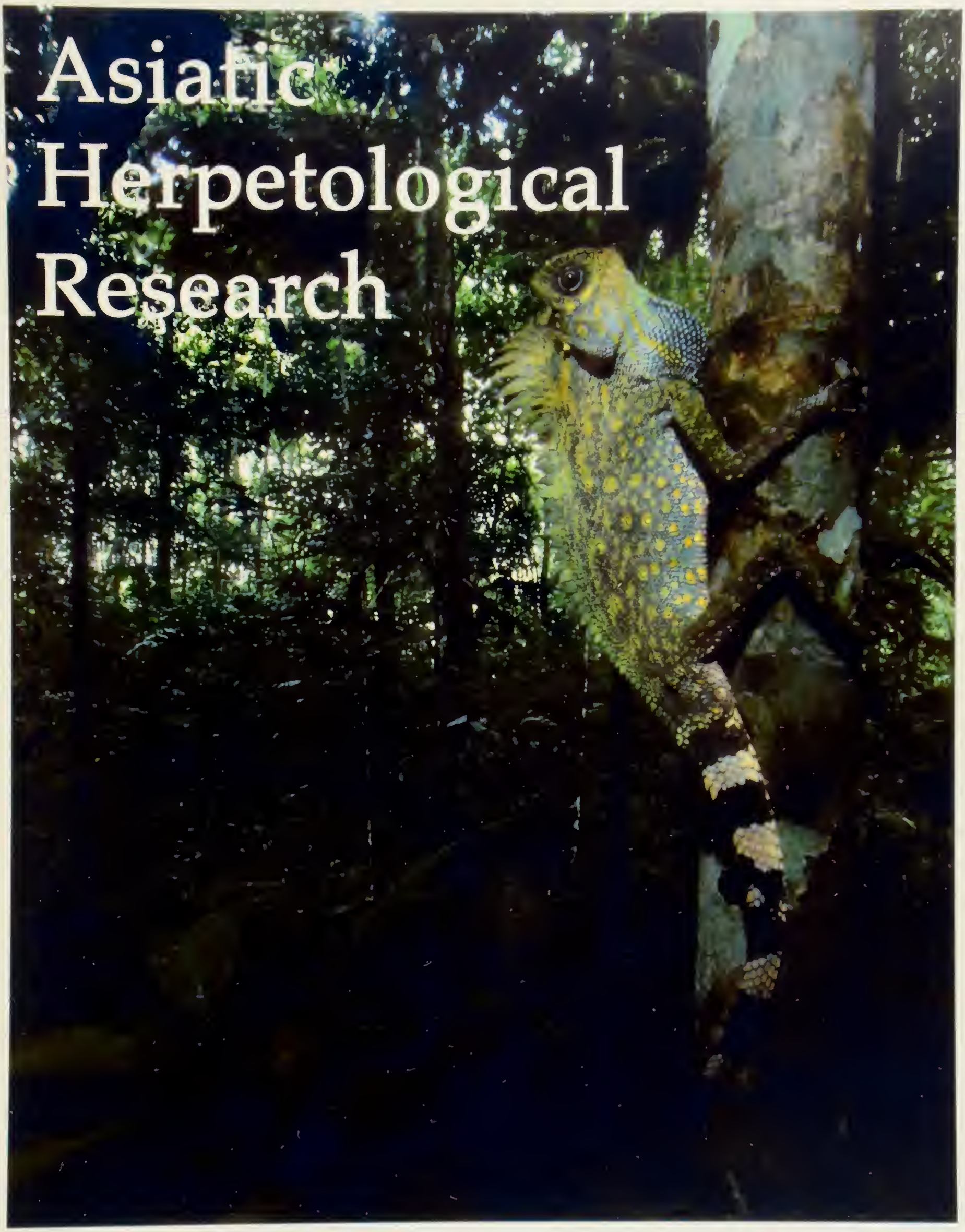

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Cover: The cover image is of *Gonocephalus chamaeleontinus* from Pulau Tioman, Pahang, West Malaysia. Photo by L. Lee Grismer.

A New Species of *Dibamus* (Squamata: Dibamidae) from West Malaysia

RAUL E. DIAZ[1,2,*], MING TZI LEONG[3], L. LEE GRISMER[1], AND NORSHAM S. YAAKOB[4]

[1]*Department of Biology, La Sierra University, Riverside, CA 92515-8247, USA*
[2]*Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA*
**Corresponding author E-mail: rauldiaz@berkeley.edu*
[3]*Department of Biological Sciences, National University of Singapore, Kent Ridge, Singapore 119260, Republic of Singapore*
[4]*Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia*

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Abstract. - A new lizard of the genus *Dibamus* is described from Pulau Tioman and Pulau Tulai, Pahang, West Malaysia. This species most closely resembles *D. novaeguineae, D. kondaoensis, D. leucurus and D. montanus*, but differs from all congeneric species in exhibiting the following combination of characters: postoculars 1, scales bordering first infralabial 4, SVL 123 mm, 25-26 midbody scale rows, frontonasal and rostral sutures complete, and the presence of slightly posteriorly notched cycloid body scales as an adult.

Key words. - *Dibamus, Dibamus tiomanensis*, new species, Dibamidae, Pulau Tioman, West Malaysia.

Introduction

The genus *Dibamus* presently contains 18 species (see Greer, 1985; Darevsky, 1992; Das, 1996; Honda et al., 1997; Ineich, 1999; Honda et al., 2001; Das and Lim, 2003; Das and Yaakob, 2003), a two-fold difference from the detailed review of the group by Greer (1985). Species of the genus *Dibamus* collectively range throughout southeast Asia, from southern China and the Philippines through Indonesia. *Dibamus alfredi* was described by Taylor (1962) from Thailand. *D. alfredi* were later found on the island of Nias, off the west coast of Sumatra (Greer, 1985) and from Danum Valley in Sabah State, Borneo (Tan, 1993; Das and Yaakob, 2003). A large gap was then left between Thailand and Borneo. Lim and Lim (1999) reported *D.* cf. *alfredi* from Pulau Tioman. Upon examination of their specimen, one from Pulau Tioman, and another from P. Tulai, we conclude that these specimens constitute a new species described herein. Pulau Tioman lies between longitudes 104° 7' to 104° 15' E and latitudes 2° 44' to 2° 54' N (Bullock and Medway, 1966). Finding another endemic population on this island provides another reason for its conservation as well as further studying its rich herpetofauna.

Material and Methods

Single females from both Pulau Tulai and Pulau Tioman were collected, fixed in 10% formalin, and preserved in 70% ethanol. Both specimens were deposited in the Zoological Reference Collection (ZRC) at the Raffles Museum of Biodiversity Research. Sliding calipers were used for all length measurements. Terminology used follows Greer (1985) and Honda et al. (1997). Individuals were sexed externally under a dissecting microscope; males were identified by having two small, flap-like limbs (one on each side of the vent) (Duméril and Bibron, 1839).

Taxonomy

Dibamus tiomanensis, new species
Figs. 1, 2

Holotype. - ZRC.2.3410, adult male collected at Kampung Paya, Pulau Tioman, Pahang, West Malaysia (Fig. 2) on 16 September 1995.

Paratypes. - Adult female (ZRC 2.5092) collected along the trail to Bukit Bakau, Pulau Tulai, West Malaysia (Fig. 2) collected 14 July 2001. Juvenile female (ZRC.2.5260) collected along the Tekek-Juara Cross Island Trail, Pulau Tioman, West Malaysia collected 11 July 2001.

Diagnosis. - *Dibamus tiomanensis* differs from all other species of *Dibamus* in having cycloid scales which are slightly notched posteriorly as an adult and flat cycloid light brown dorsal scales with cream borders as a juvenile. It also differs from other *Dibamus* in having the following combination of characters: rostral sutures incomplete; nasal and labial sutures complete; scales bordering posterior edge of first infralabial 4; postocular 1; transverse scale rows just posterior to head 29, at midbody 25, proximally anterior to vent 21; subcaudals 45; snout blunt in lateral profile (Fig. 1; Table 1); presacral vertebrae 124; postsacral vertebrae 23 (Table 3).

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Figure 1. Photograph of *Dibamus tiomanensis*, new species, on forest leaf litter.

Description of holotype. - Snout-vent length 92.5 mm; tail length 13.1 mm; midbody diameter 2.5 mm. Snout bluntly rounded; nostril lateral; rostral pad with large number of evenly distributed sensory papillae; rostral sutures incomplete; nasal sutures complete from nostril to ocular; labial sutures complete from anterior part of nasal suture to mouth; frontonasal six times wider than long; frontal approximately 1.05 times wider than frontonasal; interparietal bordered posteriorly by four slightly smaller nuchal scales; postocular one; supralabial one; scales bordering posteromedial edge of first infralabial four; ear opening absent; eyes dimly visible through ocular; body scales notched posteriorly; transverse scale rows just posterior to head 23, at midbody 25, at just anterior to vent 23; subcaudals 50; tip of tail blunt, not terminating in a spine; hind limb length 2.6 mm.

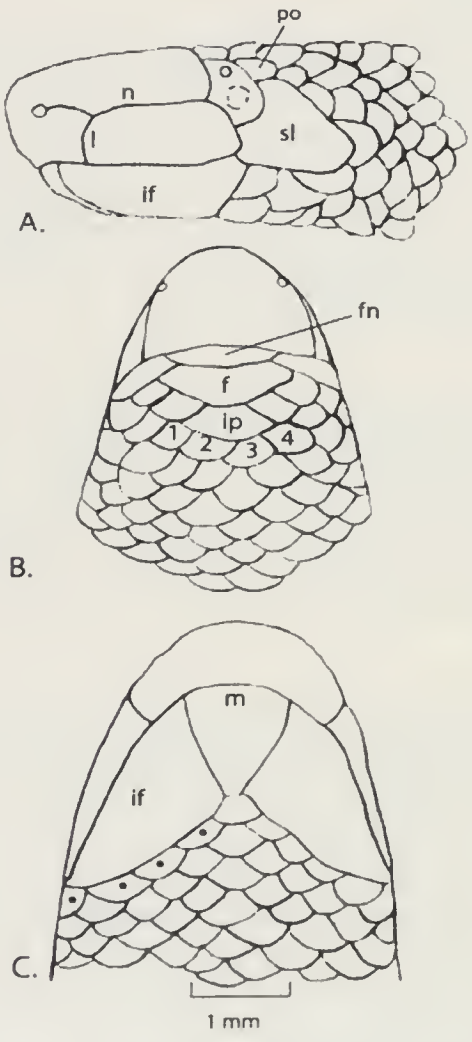

Figure 2. Lateral (A), dorsal (B), and ventral (C) view of head of *Dibamus tiomanensis*, new species. (f: frontal, fn: frontonasal, ip: interparietal, if: first infralabial, l: labial suture, m: mental, n: nasal suture, o: ocular, po: postocular, sl: supralabial)

Description of paratypes. - The paratypes (both females) are similar to the holotype in all aspects except the following: transverse scale rows posterior to head 29, transverse scale rows anterior to vent 21 and 22, and subcaudals 45 and 48.

Variation. - Paratype ZRC.2.5260 is the only juvenile. It shows a possible ontogenetic change in scale morphology. Juveniles have cycloid, flat, and light brown-cream bordered scales. Adults have posteriorly notched brown scales.

Color in life. - Adults have a brown ground color both dorsally and ventrally, except on the snout and jaws which are a lighter shade of brown. Juveniles have a cream-colored snout and jaws which contrast well with the darker spotted sensory papillae and body scales which are light-brown bordered with cream. Manthey and Grossman (1997:205) present a color photograph of the holotype.

Table 1. Comparison of several scale characters and measurements within *Dibamus*. The size of the frontal is measured relative to the frontonasal and the interparietal relative to the surrounding anterior body scales. Sample sizes for postoculars and scales on posterior edge of infralabials are given in parentheses. Entries for midbody scale rows and subcaudal scales are as follows from top to bottom: range, mean, and sample size (modified from Greer, 1985). (*= 1 & 3 refer to 1 scale present on the left infralabial and 3 on right; **=tail regenerated; *** = text in Das and Yaakob (2003) mentions 3 scales bordering the infralabials in diagnosis, whereas 4 scales are mentioned in description of holotype).

Dibamus	Post-oculars	Scales on posterior edge of infralabial	Mid-body scale rows	Subcaudal Scales		Relative size of:		Max. SVL	Tail Length (% of SVL)
				Males	Females	Frontal	Interparietal		
alfredi	2(4)	3(3) 4(1)	20-21 20.3 3	46-47 46.5 2	41-46 43.5 2	1.4-2.0	1.7-2.2	135	17-18
bogadeki	1(1)	2(1)	23 23 1	51 51 1	-	-	-	177**	22.5
booliati	1(2)	3(2)***	20 20 1	-	24-39 31.5 2	-	-	102.7	9.4-13.0
bourreti	1(1)	2(1)	24 24 1	-	52+ 52+ 1	2.3	4.5	151	23+
celebensis	2(10) 3(3)	3(6) 4(7)	26-30 27.4 13	38-40 39.3 3	35-40 38.0 4	1.2-2.3	1.0-2.9	188	10-13
deharvengi	1(1)	2(1)	16 16 1	57 57 1	-	1.3	1.4	92	22.4
greeri	1(3)	1&3(2)*	20 20 1	53 53 1	54 54 1	-	-	86	23-28
ingeri	2(1)	3(1)	20 20 1	36 36 1	-	1.5	1.0	96	14.8
kondaoensis	2(1)	3(1)	23 23 1	59 59 1	-	1.03	1.0	112.4	19.4
leucurus	1(23)	3(21) 4(2)	20-23 21.0 23	48-52 49.5 4	41-47 43.5 4	1.2-4.2	1.0-3.1	136	16-20
montanus	1(2)	2(2)	22 22 2	49 49 1	43 43 1	2.0	2.2	130	15-18
nicobaricum	1(6)	4(6)	23-25 24.6 6	34-38 35.6 3	31-36 34.3 3	-	-	134.7	8.7-18.3
novaeguineae	2(92) 3(2)	3(53) 4(41) 5(1)	22-26 24.5 107	42-45 43.0 6	37-42 39.6 9	1.0-3.0	0.7-2.4	158	9-19
seramensis	4(1)	4(1)	33 33 1	-	40 40 1	0.7	1.2	203	11
smithi	1(1) 2(4)	2(5)	18-19 18.8 5	59 59 1	59-61 60.0 3	1.5-2.3	1.3-2.0	108	21-24

Table 1. Continued.

Dibamus	Post-oculars	Scales on posterior edge of infralabial	Mid-body scale rows	Subcaudal Scales Males	Subcaudal Scales Females	Relative size of: Frontal	Relative size of: Interparietal	Max. SVL	Tail Length (% of SVL)
somsaki	1(4)	2(4)	18-19 18.5 4	44**-58 51 2	27**-57 42 2	1.1-1.27	1.0-2.16	106	18-24
taylori	3(13) 4(6)	2(2) 3(14) 4(4)	22-28 23.4 22	41-55 48.4 5	41-52 48 7	0.2-1.3	1.0-1.2	169	14-19
tiomanensis	1(3)	4(3)	25-26 25.3 3	50 50 1	45-48 46.5 2	1.2	1.8	123	15-16
vorisi	2(2)	3(2)	20 20 2	33 33 1	11 11 1	1.2	1.0	89.2-90.1	6.1-16.8

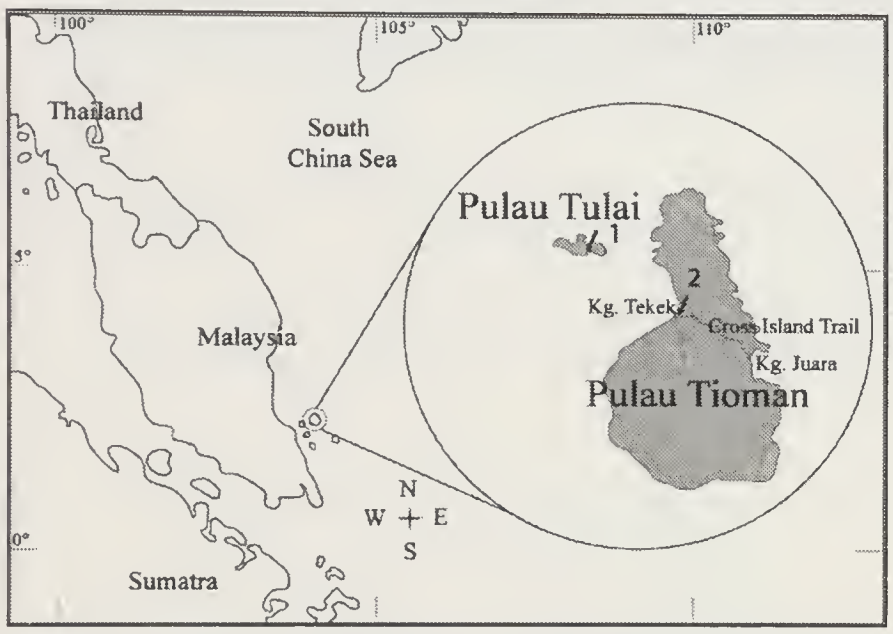

Figure 3. Map of Southeast Asia showing the distribution of known *Dibamus tiomanensis* specimens. (1) Trail to Bukit, Pulau Tulai, (2) Tekek-Juara Cross island trail on Pulau Tioman (from Kg. Tekek to Kg. Juara)

Etymology. - This species is named after the type locality for the holotype (Pulau Tioman = Tioman Island)

Distribution. - Endemic to Pulau Tioman and adjacent Pulau Tulai (Fig. 2).

Comparisons. - *Dibamus tiomanensis* was listed as *D.* cf. *alfredi* owing to its geographic proximity to *D. alfredi*, which occurs in Peninsular Malaysia and Thailand (Manthey and Grossman, 1997; Taylor 1963). The presence of four scales bordering the first infralabial posteriorly differentiates the new species, *Dibamus tiomanensis*, from *D. bogadeki*, *D. booliati*, *D. bourreti*, *D. deharvengi*, *D. greeri*, *D. ingeri*, *D. kondaoensis*, *D. montanus*, *D. smithi*, *D. somsaki*, and *D. vorisi*. In having one post ocular present, *D. tiomanensis* differs from *D. alfredi*, *D. celebensis*, *D. novaeguineae*, *D. seramensis*, and *D. taylori*. From the remaining two congeners, *D.*

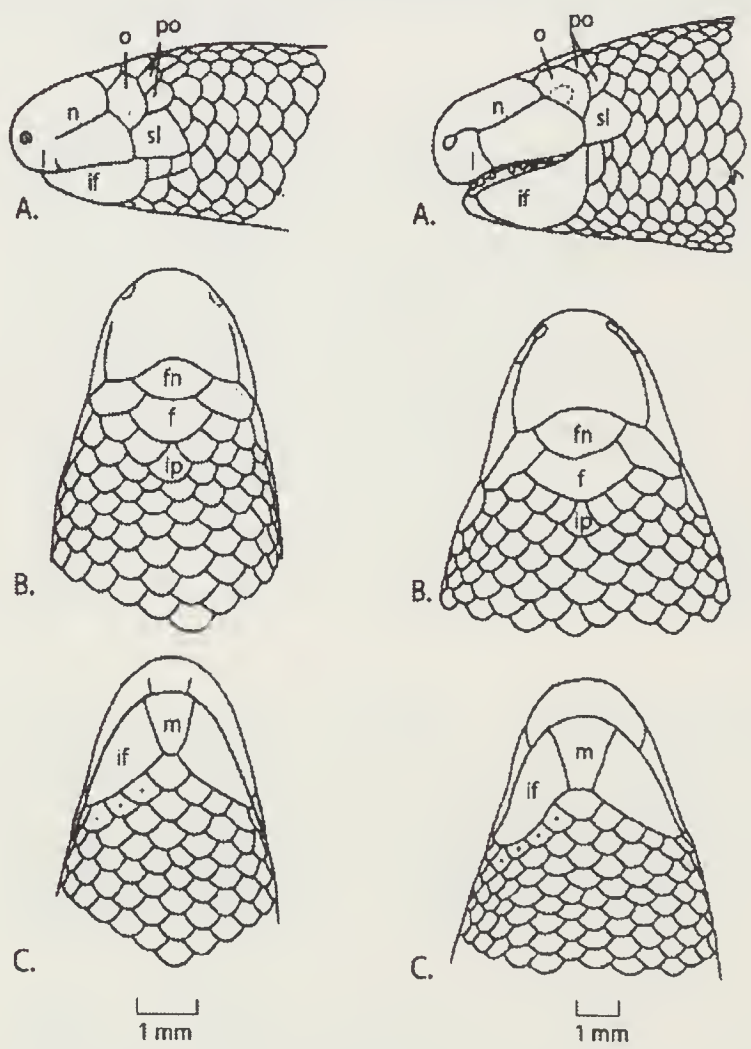

Figure 4. Lateral (A), dorsal (B), and ventral (C) view of heads of *Dibamus alfredi* (left) and *Dibamus novaeguineae* (right). Figures from Greer (1985). [f: frontal, fn: frontonasal, ip: interparietal, if: first infralabial, l: labial suture, m: mental, n: nasal suture, o: ocular, po: postocular, sl: supralabial]

tiomanensis differs from *D. montanus* Smith, 1921 (Langbian Plateau, Vietnam) in having more pre-sacral vertebrae (124 vs. 112-114) and *D. leucurus* (Bleeker, 1860) (Sumatra, Borneo) in the presence of slightly posteriorly notched cycloid scales as an adult.

Table 2. Matrix of diagnostic characters and their states for species of *Dibamus* (modified from Greer, 1985).

Dibamus	Rostral suture complete and separate (+), complete and meeting (-), incomplete (0) or absent (1)	Nasal suture complete (+), reduced (-), or absent	Labial suture complete (+), incomplete dorsally to varying degrees (-), or absent (0)	First infralabial surrounded by 1(+), 2 (-), 3(0), 4(1), or 5(2) scales	No. of post ocular scales 1(+), 2(-), 3(0), or 4(1)	Body scales cycloid (+) or cycloid and slightly knotched posteriorly (-) in adults
alfredi	0	-	-	0,1	-	+
bogadeki	0	+	+	-	+	+
booliati	1	-	+	-	+	+
bourreti	+	+	0	-	+	+
celebensis	0	+	+	0,1	-,0	+
deharvengi	-	+	+	-	+	+
greeri	0	-	+	0*	+	+
ingeri	0	+	+	0	-	+
kondaoensis	0	+	+	0	-	+
leucurus	0	-	+	0,1	+	+
montanus	-	+	+	0	+	+
nicobaricum	+	+	+	1	+	+
novaeguineae	0	+	+	0,1,2	-,0	+
seramensis	0	+	+	1	1	+
smithi	0	-	0	-	+,-	+
somsaki	-	+	+	-	+	+
taylori	0	+	+	-,0,1	0,1	+
tiomanensis	0	+	+	1	+	-
vorisi	0	+	0	0	-	+

* = See Table 1 for information on this character state.

D. nicobaricum is included in this study following Das' (1996) redescription and reevaluation of the species (in which it is inaccurately referred to as *D. nicobaricus* through parts of the paper) despite Honda et al. (2001) avoidance of it's recognition as a nominate species.

Great difficulty arises in finding specimens of Dibamus for study due to their fossorial lifestyle. As a result, many descriptions are based on 2-5 individuals. An unusually large collection of *D. novaeguineae* from Mt. Canlaon, Negros Island, Philippines (Greer, 1985:150) has given a unique insight to how variable morphological characters can be within a single population (See Table 1). Further studies are needed in studying variation within this family as slight character state variances have warranted the recognition of new species [See Das and Lim (2003), Das and Yaakob (2003), and this paper] which may prove to be a variant of an already described taxon.

Table 3. Sacral vertebrae count of described species of *Dibamus*.

Dibamus	Sacral vertebrae pre-sacral	post-sacral
alfredi	116-126	22-26
bogadeki	134	25
booliati	113-120	11-25
bourreti	115-129	12-40+
celebensis	117-132	17-22
deharvengi	120	36
greeri	96-111	28-31
ingeri	97	21
kondaoensis	140	33
leucurus	106-135	21-28
montanus	112-114	24-27
nicobaricum	124	23
novaeguineae	109-125	18-24
seramensis	130	18
smithi	130-137	30-34
somsaki	119	31
taylori	112-135	21-29
tiomanensis	124	23
vorisi	97	20

Natural History

The holotype was found under a large stone in Kampung Paya, Pulau Tioman. ZRC 2.5092 was found beneath leaf litter in loose dirt adjacent to a large rock and bamboo stands in secondary forest along the trail to Bukit Bakau on Pulau Tulai at 20 m elevation. ZRC.2.5260 was found beneath a decaying log one meter from the cross-island trail in primary forest on Pulau Tioman.

Adult *Dibamus tiomanensis* displayed a behavior most likely intended to ward off a predator. When picked up or startled, the body scales flare up at an angle almost perpendicular to the body. When viewed, the smooth surface appears rugose, resembling the bristle-covered epidermis of an earthworm. It is possible that a non-palatable species of worm exists in the same area and has served as a model for *D. tiomanensis* to mimic. Darevsky (1992) mentions that *D. greeri* has bright blue rings on its body, perhaps mimicking a megascolicid worm inhabiting the same leaf litter. Such mimicking behavior was also recently reported in *D. booliati* (Das and Yaakob, 2003).

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A New Species of *Leptolalax* (Anura: Megophryidae) from Pulau Tioman, West Malaysia

L. Lee Grismer, Jesse L. Grismer, and Timothy M. Youmans

Department of Biology, La Sierra University, Riverside, CA 92515-8247

Abstract. - A new species of *Leptolalax* is described from a cave at the top of Gunung Kajang, Pulau Tioman, Pahang, West Malaysia. It differs from all other Malaysian species of *Leptolalax* in several aspects of coloration and in having smooth as opposed to rough or pebbled skin on the dorsum.

Key words. - *Leptolalax*, Anura, Tioman, Malaysia.

Introduction

There are at least eight species of *Leptolalax* found throughout West Malaysia and Borneo (Berry, 1975; Inger et al., 1995; Inger et al., 1997; Matsui, 1997) but only one of these, *L. gracilis*, is known from both regions. In an unpublished document, Day (1990) reported *Leptobrachium* sp. from Pulau Tioman, Pahang, West Malaysia based on five larvae collected in the Tengkuk Air Cave (Gua) at 1000 m elevation on Gunung Kajang. Lim and Lim (1999) referred these larvae to *Leptolalax gracilis* based on three additional larvae they collected at a lower elevation (ca. 400 m) on Gunung Kajang. More recently, Grismer et al. (2004) reported two adults from Gua Tengkuk Air. Examination of those adults indicates that they belong to the genus *Leptolalax* not *Leptobrachium* (but they are not *L. gracilis)*. We therefore, refer these specimens and the larvae of Lim and Lim (1999) to the new species described herein.

Materials and Methods

The following measurements were made with sliding calipers to the nearest 0.1 mm: adults; snout-vent length (SVL), tibial length (TL), head width (HW), head length (HL), and diameter of tympanum (TYM). Tadpoles (Table 1); interorbital distance (IOD), internarial distance (IND), tail length (TL), and tail height (TH). Tadpoles were preserved in 10% formalin and transferred to 70% ethanol. Due to shrinking and wrinkling, head-body width (HBW), head-body height (HBH), and tail height (TH) are likely to be underestimated. Observations on external morphology were made with the use of a dissecting microscope. Specimens were compared to material listed in Appendix I and descriptions in Berry (1975), Inger (1985), Inger et al. (1997), Inger et al. (1995), Inger and Stuebing (1997), Malkmus (1992), and Matsui (1997).

***Leptolalax kajangensis*, new species**
(Figs. 1-2)

Holotype. - ZRC 1.7714; adult male, 34.0 mm SVL; found inside Gua Tengkuk Air, Gunung Kajang, Pulau Tioman, Pahang, West Malaysia at 1000 m in elevation. Collected by Jesse L. Grismer and Timothy M. Youmans on 21 July, 2001.

Paratype. - ZRC 1.7715; adult male, 35.0 mm SVL. Same data as holotype.

Diagnosis. - *Leptolalax kajangensis* differs from all other Malaysian species of *Leptolalax* in lacking distinct dark crossbands on the limbs and having a generally dark, unicolor to weekly patterned dorsum. It differs further from *L. arayai*, *L. dringi*, *L. gracilis*, *L. hamidi*, and *L. maurus*, in having smooth, as opposed to rough, warty skin. It differs further from *L. dringi*, *L. gracilis*, and *L. heteropus* in lacking dark spots on the ventrum. It differs further from *L. gracilis* and *L. hamidi* in lacking a dark inguinal blotch and from *L. gracilis* in lacking a distinctly bicolored forelimb and dark markings on the ventral surface of the foreleg.

Description of holotype. - Habitus moderately slender, head longer than wide; snout rounded in dorsal profile, weakly projecting beyond lower jaw; nostrils raised, directed dorsolaterally, and situated on canthi, near tip of snout; canthi rounded; lores slightly oblique; eye large, diameter slightly longer than length of snout; internarial distance less than interorbital distance; interorbital width slightly greater than length of snout; tympanum visible, less than one-half diameter of eye, separated from eye by width of tympanum; vomerine teeth absent; tongue notched, without papillae.

Forelimbs slender; fingers slender, unwebbed, tips rounded; first finger equal in length to second; no subarticular tubercles or elongate cornified pads visible beneath fingers; large inner palmar tubercle present and

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Figure 1. Photograph of *Leptolalax kajangensis*, new species, on forest leaf litter.

much smaller outer palmar tubercle at base of fourth digit.

Hindlimbs relatively short; heels overlap when limbs flexed; tibiotarsal articulation of adpressed limb reaches tip of snout; tips of toes rounded; third and fifth toe equal in length; slight webbing between first and second and second and third toes only; oval inner metatarsal tubercle present; subarticular tubercles absent.

Skin on back smooth to faintly pebbled; flanks faintly pebbled; limbs smooth to faintly pebbled; prominant supratympanic fold extending from eyelid to shoulder; ventral surfaces smooth.

Coloration. - In life and ethanol, dorsal surfaces almost black with no visible pattern except for minute, faint, light-colored spots; limbs slightly lighter with faint dark mottling; faint dark mottling on flanks blending to grayish dusty ventral surfaces punctated by minute gray spots. Supratympanic fold darker than dorsum. Iris metallic gold in life.

Measurements of holotype. - SVL 34.0 mm; TL 14.2 mm; HW 18.5 mm; HL 10.0 mm; TYM 1.6 mm.

Variation. - The paratype closely approximates the holotype in all aspects of coloration and morphology. It differs in the following measurements: SVL 35.0 mm; TL 14.6 mm; HW 19.4 mm; HL 9.4 mm TYM 1.8 mm.

Etymology. - This species is named after the type locality of Gunung Kajang, Pulau Tioman, West Malaysia

Tadpoles. - Table 1 lists measurements, growth stages, and tooth row formulae of tadpoles. Based on specimens (ZRC 1.3339-41); stages 30, 36, and 37 (Gosner, 1960) from a small stream at 333 m below Gua Tengkuk Air on G. Kajang and specimens (0051-54 uncatalogued specimens in the British Museum reported by Day, 1990) stage 30 (Gosner, 1960) from Gua Tengkuk Air. Head and body relatively large and round; nostrils dorsally located, closer to tip of snout than eye; eyes dorsolateral, not visible from below; spiracle sinistral, nearer to eye than vent; vent dextral, opening at margin of ventral fin; dorsal fin slightly deeper than ventral fin, not extending onto head-body; fins not deeper than caudal musculature; oral apparatus not emarginate; mouth subterminal; bordered by a single row of conical papillae; large submarginal papillae without denticles; jaw sheaths black, robust, strongly arched, and finely serrated; upper jaw lacking medial notch; denticles small; rows A1 and P5 markedly shorter than adjacent rows. Tadpoles (ZRC.1.3339-41) from stream dusky brown above with faint darker mottling; venter cream colored, nearly immaculate; faint dark stippling on caudal fins, edges clear and immaculate; lateral line hash marks distinct. Tadpoles from Gua Tengkuk Air (uncatalogued BM specimens) lack pigment and are white to transparent in life.

Comparisons with other species. - *Leptolalax kajangensis* differs from all other Malaysian species of *Leptolalax* on the basis of skin surface texture and coloration. *Leptolalax arayai*, *L. dringi*, *L. gracilis*, *L. hamaidi*, *L. maurus*, and *L. pelodytoides* all have coarsely textured skin ranging from distinctive corrugations in

Table 1. Selected measurements (mm), growth stage (GS), and labial tooth row formulae (LTRF) of *Leptolalax kajangensis*. Abbreviations follow Materials and Methods. * = Specimen damaged.

Cat. no.	HBW	HBL	HBH	IOD	IND	TL	TH	GS	LTRF
0051	13.5	23.3	8.4	4.8	3.2	39.9	10.0	30	6(2-6)/5(1-4)
0052	15.2	23.8	9.3	6.6	4.9	49.9	13.7	38	6(2-6)/5(1-4)
0053	13.5	23.5	10.0	5.0	4.3	*	*	30	6(2-6)/5(1-4)
0054	14.5	25.5	10.0	5.4	3.9	45.5	11.0	30	6(2-6)/5(1-4)
0055	14.1	25.9	10.0	6.7	4.8	43.5	12.0	38	6(2-6)/5(1-4)
ZRC.1.3339	11.2	23.5	8.2	6.0	2.6	41.4	*	30	6(2-5)/5(2-4)
ZRC.1.3340	19.6	30.8	14.5	7.3	4.5	56.4	*	35	6(2-6)/1(1-3)
ZRC.1.3341	18.0	31.9	14.2	7.8	4.6	51.9	*	36	5(4)/4(1-3)

Figure 2. Tadploe of *Leptolalax kajangensis* at type locality.

L. dringi to isolated tubercles of varying sizes in *L. gracilis* (Inger and Stuebing, 1997; Inger et al. 1997; Matsui, 1997). *Leptolalax kajangensis* resembles *L. pictus* and *L. pelodytoides* in having smooth to weakly pebbled skin on the dorsum (Inger et al. 1995) but differs from *L. pictus* in lacking small tubercles on its sides (Malkmus, 1992). *Leptolalax kajangensis* falls within the size range (SVL 34.0-35.0 mm) of *L. dringi* (SVL 30.0-38.8 mm), *L. gracilis* (SVL 31.0-48.0 mm), *L. heteropus* (SVL 33.0-35.0 mm), *L. pelodytoides* (SVL 30.0-42.0 mm), and *L. pictus* (SVL 31.0-47.0 mm) but is larger than *L. arayai* (SVL 29.9) and *L. marus* (SVL 26.0-32.0). *Leptolalax kajangensis* differs most notably from other species in coloration. Its generally unicolor black dorsal pattern contrasts sharply with the various mottled body patterns of *L. dringi*, *L. hamidi*, *L. heteropus*, *L pelodytoides*, and *L. pictus*. It does resemble *L. maurus* to some extent in that *L. maurus* has a black unicolored dorsum but differs in that the latter also has lighter colored limbs with darker crossbars and light colored spots on the flanks, patterns which are absent in *L. kajangensis*. *Leptolalax gracilis* also has a generally dark dorsal coloration with varying degress of dark mottling but is distinctive in having a light colored brachium. The single specimen of *L. arayi* has a light ground color with darker crossbands on the limbs.

Natural history. - Both specimens of *Leptolalax kajangensis* were found in a cave (Gua Tengkuk Air) near the summit of Gunung Kajang at approximately 1000 m in elevation. This subterranean, obliquely oriented cavern is formed from the overhang of large boulders piled on top of one another. It contains a small pond (3 m x 4 m) drained by a small subterranean stream (1-3 m in width by 2-4 cm in depth) running for 3-4 m along the cave floor. Both specimens of *L. kajangensis* were observed in the afternoon sitting on top of large rocks adjacent to the stream approximately 10 m from the entrance to the cave and approximately 10 m below the outside ground level. It was from the subterranean pond that Day (1990) collected "large tadpoles" he referred to as *Leptobrachium* sp. We observed additional tadpoles and assume these to be larvae of *Leptolalax kajangensis* based on the fact that the type material were collected from the same stream and adults were observed calling from the edge of the pond.

Three additional larvae examined here (ZRC.1.3339-41) were collected from a lower stream on Gunung Kajang at approximately 400 m on 26 June 1996 (Lim and Lim, 1999). We tentatively assign these to *Leptolalax kajangensis* because they match the larvae from Tengkuk Air in morphology (Table 1). However, the Tengkuk Air specimens lack pigment and are white to transparent in life (Fig. 2). ZRC.1.3339-41 are countershaded with dark pigment above and have minute dark flecks on a light venter. This indicates that either *L. kajangensis* is not confined to only the upper most elevations of Gunung Kajang or that there may be an additional species of *Leptolalax* found lower down on the mountain.

Biogeography. - Pulau Tioman had a land positive connection with Peninsular Malaysia as late as the Pleistocene (Voris, 2000). The presence of amphibian species on Pulau Tioman such as *Leptolalax kajangensis*, *Megophrys nasuta*, *Rana hosii*, *R. picturata* and others that require streams with moderate to strong currents for reproduction suggests these species are unlikely candidates for long distance dispersal over flat, low-lying landscape (Inger and Voris, 2001). Pulau Tioman was part of a large granitic arc of mountains extending from what is currently peninsular Malaysia through the Kepulauan Anambas and Natunas across the Greater Sunda Shelf which provided a dispersal corridor for montane species (Inger and Voris, 2001) across the flat, low-lying exposed Sunda Shelf. Thus, the presence of stream-breeding species requiring moderate to fast flowing water on Pulau Tioman is most likely a result of vicariance.

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A New Species of Kukri Snake, *Oligodon* (Colubridae), from Pulau Tioman, West Malaysia.

TZI MING LEONG[1] AND L. LEE GRISMER[2]

[1]*Department of Biological Sciences, National University of Singapore, Singapore 119260*
[2]*Department of Biology, La Sierra University, Riverside, California 92515-8247, USA*

Abstract. - A unique species of *Oligodon* is described from the type locality of Pulau Tioman, West Malaysia. In terms of scalation, it is most comparable with the Bornean *O. subcarinatus*, but does not exhibit any feeble keeling of scales. In addition, its body color and patterns are unique in having a red dorsum, pink ventral surface, and indistinct pale bars on the nape and body.

Key words. - *Oligodon*, kukri snake, Pulau Tioman, West Malaysia.

Introduction

The kukri snakes belonging to the genus *Oligodon* Boie, 1827 are so named because of the presence of unique posterior maxillary teeth, shaped like Ghurka kukri knives. In addition, members belonging to this genus are small to medium-sized ground dwelling species characterised by having a large slightly upturned rostral shield, short head, round pupil, and a cylindrical body with smooth scales (Tweedie, 1983; Cox et al., 1998). Many species possess a distinct dark chevron mark on the nape and a stripe across the anterior part of the head and down over/through the eye. Although *Oligodon* is well represented in South and Southeast Asia, there are only three species on Peninsular Malaysia, namely *O. octolineatus* Schneider, *O. purpurascens* Schlegel, and *O. signatus* Günther (Tweedie, 1983). In Borneo, eight species have been recorded [*O. annulifer* Boulenger, *O. cinereus* Günther, *O. everetti* Boulenger, *O. octolineatus* Schneider, *O. purpurascens* Schlegel, *O. signatus* Günther, *O. subcarinatus* Günther, and *O. vertebralis* Günther]. However, the occurrences of true *O. annulifer* and *O. cinereus* on Borneo remain to be verified (Stuebing and Inger, 1999).

On Pulau Tioman, ca. 40 km from the southeast coast of the peninsula, one species (*O. purpurascens)* has been reliably recorded thus far (Grismer et al., 2004; Hendrickson, 1966). The presence of *O. octolineatus* on the island, though possible, remains to be verified (Lim and Lim, 1999). Day (1990: 38) reported the presence of a distinct, new form of *Oligodon* from the cross-island (Tekek-Juara) trail, but did not provide any diagnostic characters. It was merely mentioned that this form resembled *O. signatus*, but had differences in terms of head scalation and dorsal colouration. We collected a specimen from the same locality on 16 July, 2001 that is different from all other nominal species of Malaysia and is herein named and described as new.

Materials and Methods

Prior to preservation in 10% formaldehyde, the specimen was photographed and liver tissue sampled. Total length, tail length, and snout-vent length were obtained using a measuring tape (to nearest 1 mm). Additional measurements taken, using vernier callipers (to nearest 0.1 mm), include eye diameter (ED); head length (HL), taken from the union of the posteromedial corners of the parietals to the tip of the snout; head depth (HD), taken from the dorsal surface of the head to the ventral surface of the jaw immediately posterior to the eye; and snout length (SL), taken from the anterior margin of the eye to the tip of the snout. The scale counts included upper labials, number of upper labials in contact with eye, lower labials, preoculars, postoculars, ventrals, subcaudals, and midbody scales. Comparative material was examined from the Zoological Reference Collection (ZRC) [Raffles Museum of Biodiversity Research (RMBR), National University of Singapore], the Department of Wildlife and National Parks, Peninsular Malaysia (DWNP) herpetological collection, the Bishop Museum, Hawaii (BPBM), and Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (ZMB).

Oligodon booliati, sp. nov.

Holotype: ZRC.2.5153, adult female, collected on the night of 16 July, 2001, at 2130 hrs by T. M. Leong and K. M. Crane, while it was crawling on a concrete staircase in primary forest along the Tekek-Juara trail, ca. 150 m asl., Pulau Tioman (Pahang, Peninsular Malaysia). Deposited at the Zoological Reference Collection (ZRC).

Paratypes: (1) BPBM 13933, subadult male, collected on 17 April 1962 by J. R. Hendrickson, at Ulu Lalang,

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Figure 1. Dorsal view of *Oligodon booliati* holotype, ZRC.2.5153 (live coloration).

ca. 700 m asl and (2) ZMB 64446, adult female, collected in May 2001 by W. Grossmann and C. Scafer on the top of the Tekek-Juara Trail at 300 m asl.

Diagnosis. - 6-7 upper labials, 2nd and 3 rd or 3rd and 4th touching eye, 7 lower labials, 17 mid-body scales, 143-153 ventrals, 54-60 subcaudals. Loreals present. Head scales without distinct patterns. No distinct stripe running through eye. In life, body deep maroon red dorsally and along flanks, salmon pink on the ventrals and subcaudals. Ventrals without dark spots. Indistinct dark brown transverse bars (19-22) on body, starting from nape and fading increasingly towards tail. Thin, dark brown stripes on anterior sides of 5th and 6th upper labials, immediately posterior to eye.

Description of Holotype. - Adult female, total length: 510 mm, tail: 121 mm, snout-vent: 389 mm, ED: 2.2 mm, HL: 10.8 mm, HD: 6.9 mm, SL: 5.0 mm; head stout (HD/HL 0.64), slightly broader than neck; snout moderate, oblique in dorsal profile, oval in lateral profile; eye 20% of head length, pupil round; rostral shield large, triangular, visible from above, width (3.5 mm) greater than height (3.0 mm), concave below; rostral in direct contact with first upper labials, nasals and internasals; trapezoid prefrontals posterior to internasals, curving at canthus rostrals to meet triangular postnasals; single, almost triangular frontal, slightly longer (4.8 mm) than wide (4.2 mm), posterior point terminating 1.2 mm beyond posterior margin of eye; frontal flanked by prominent supraoculars, length of supraocular (3.0 mm) 1.4 of ED; 7 upper labials, increasing in size to 6th, 3rd and 4th in contact with eye; a small (0.5 x 0.5 mm) loreal scale present on left, but absent on right, allowing contact between right prefrontal and 2nd upper labial; one preocular and one postocular present on both sides; 7 lower labials, first pair elongated transversely, confining mental to meet medially, 4th pair largest; anterior chinshields longer than (almost double) posterior chinshields; 17 scale rows at neck and midbody, but 15 at one head length anterior to vent; 143 ventrals, lateral margins visible from the sides; 59 subcaudals, all divided; anal shield single. Colour in life deep maroon red on dorsum and flanks (Fig. 1). Ventrals salmon pink, the colour becoming increasingly intense towards the tail tip (Fig. 2), without any melanistic pigmentation. Head scales without markings dorsally. Distinguishable grey-brown pigmentation visible in other head scales: dorsal portion of 4th upper labial (point of contact with eye), anterior margins of 5th and 6th upper labials, anterior margins of 1st to 4th lower labials, in between anterior chinshields towards the anterior, within mental, and lower surface of rostral. Crossbars on body faint. 21 crossbars from nape towards tail tip. Upon preservation, and storage in alco-

Table 1. Measurements, scale counts, and number of crossbars among *Oligodon booliati* sp. nov. type materials (holotype and two paratypes). L/R = Left/Right sides.

	Holotype ZRC.2.5153 Adult female	Paratype #1 BPBM 13933 Subadult male	Paratype #2 ZMB 64446 Adult female
Snout-vent length (mm)	389	260	291
Total length (mm)	510	348	373
Upper labials (L/R)	7/7	7/7	6/6
Upp. labials touching eye	3rd & 4th	3rd & 4th	2nd & 3rd
Lower labials (L/R)	7/7	7/7	7/7
Anterior nasal (L/R)	1/1	1/1	1/1
Posterior nasal (L/R)	1/1	1/1	1/1
Loreal (L/R)	1/0	1/1	1/1
Pre-ocular (L/R)	1/1	1/1	1/1
Post-ocular (L/R)	1/1	1/1	1/1
Supra-ocular (L/R)	1/1	1/1	1/1
Midbody	17	17	17
Ventrals	143	146	153
Subcaudals	59	60	54
# crossbars on body	21	22	19

Figure 2. Ventral view of *Oligodon booliati* holotype, ZRC.2.5153 (live colouration).

hol, the colours gradually faded to a lighter shade. A lateral view of the head is illustrated in Fig. 3.

Description of paratypes. - Rostral shield large, visible from above. BPBM 13933 has 7 upper labials with the 3rd and 4th touching eye. ZMB 64446 has 6 upper labials with the 2nd and 3rd touching the eye. Loreal scale (0.5 x 0.5 mm) present on both sides in BPBM 13933 and fused to the postnasal on both sides in ZMB 64446 (1.0 x 1.0 mm). One preocular and one postocular. Seven lower labials, 17 midbody scales, 146 ventrals, 60 subcaudals in BPMB 13933 and 153 ventrals and 54 subcaudals in ZMB 64446. First pair of infralabials separated medially by the mental in ZMB 64446. Total length (BPBM 13933): 348 mm; tail: 88 mm; snout-vent: 260

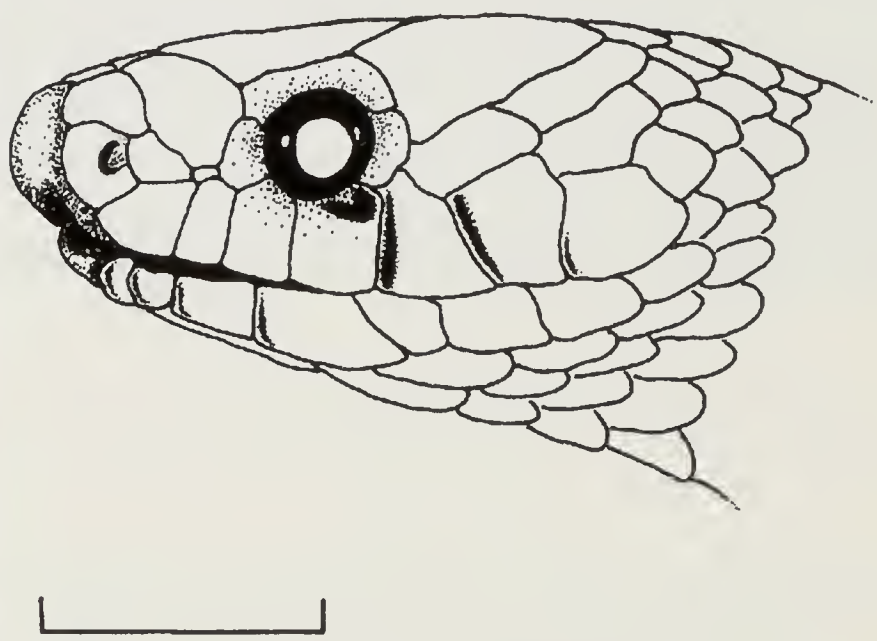

Figure 3. Lateral view of head (left side) of *Oligodon booliati* holotype, ZRC.2.5153. Scale bar = 5mm.

mm. Total length (ZMB 64446): 373 mm; tail: 82 mm; snout-vent: 291 mm. Anal shield single, subcaudals paired. Colour in preservative faded to a cream colour. No distinctly striking markings on head, faint crossbars on body (22 in BPBM 13933, 19 in ZMB 64446). Measurements and scale counts of type materials are summarised in Table 1.

Etymology. - This new species is named in honor of Lim Boo Liat, of the Department of Wildlife and National Parks (Peninsular Malaysia), whose contributions to our better understanding of Malaysia's natural history dates back to the 1950's. His publications include the description of a new snake (*Macrocalamus tweediei* Lim, 1963) and the popular reference book *Poisonous Snakes of Peninsular Malaysia* (Lim, 1982).

Table 2. Comparisons between the *Oligodon* species (arranged alphabetically) of Peninsular Malaysia and Borneo, including *Oligodon booliati* sp. nov. (measurements and scalations after Manthey & Grossmann, 1997). Lo = Loreal, UL = Upper Labials, MB = Midbody, V = Ventrals, SC = Subcaudals.

Oligodon species	Total length (cm)	Lo	UL	UL touching eye	MB	V	SC
annulifer	43	1	7-8	3 & 4	15	148-162	40-58
booliati sp. nov.	51	1	6-7	2 & 3/3 & 4	17	143-153	54-60
cinereus	73	1	7-8	4 & 5	15/17	151-185	29-43
everetti	42	1	7	3 & 4	15	138-154	46-65
octolineatus	68	1	6	3 & 4	17	155-197	43-61
purpurascens	95	1	8	4 & 5/5	19/21	160-210	40-60
signatus	60	0	7	3 & 4	17	141-157	47-59
subcarinatus	40	1	7	3 & 4	17	155-166	50-54
taeniatus	34	1	8	3-5	17	146-169	30-47
vertebralis	35	1	7	3 & 4	15	136-154	35-54

Discussion

The number of upper labials (6-7) in *Oligodon booliati* may be used to distinguish it from *O. purpurascens* (8) and *O. taeniatus* (8), although *O. annulifer* and *O. cinereus* may occasionally possess eight upper labials. *O. booliati* shares the same number of midbody scales (17) as *O. octolineatus*, *O. signatus*, and *O. subcarinatus* (instead of 15 in *O. annulifer*, *O. everetti* and *O. vertebralis*) but may be distinguished from *O. octolineatus* by the absence of any longitudinal stripes along the body, from *O. signatus* by the presence of loreal scales, and from *O. subcarinatus* by the lack of feeble keels on its scales. This new species is assumed to be endemic to Pulau Tioman. Comparisons of measurements and scalation between *O. booliati* and the other species of *Oligodon* in Peninsular Malaysia and Borneo are summarised in Table 2.

Comparative Material Examined

Oligodon bitorquatus. - ZRC.2.3875, Bandung, West Java; ZRC.2.3876, Gunong Hedjo, Cheribon, West Java; ZRC.2.3957, Pengalengan, Java.

Oligodon octolineatus. - ZRC.2.2295, 2399, 2559, 3161, 3850, 3853-3855, 3859-3860, 3865, 5058, Singapore; 3861, 3863-3864, Johor Bahru, Johor, Peninsular Malaysia; 3862, 3867, Selangor, Peninsular Malaysia.

Oligodon purpurascens. - ZRC.2.3869, Sumatra, Indonesia; ZRC.2.3877-3879, Singapore; ZRC.2.3880-3881, Pulau Gallang, Riau, Sumatra, Indonesia; ZRC.2.3882, 3884, 3885, 3887, Johor, Peninsular Malaysia; ZRC.2.3883, Forest Research Institute Malaysia, Kepong, Selangor, Peninsular Malaysia; ZRC.2.3886, 3888, Fraser's Hill, Pahang, Peninsular Malaysia; Bishop Mus. 14211, Pulau Tioman.

Oligodon signatus. - DWNP.R.0005, Forest Research Institute Malaysia, Kepong, Selangor, Peninsular Malaysia; ZRC.2.4159, Bukit Asahan, Malacca, Peninsular Malaysia; ZRC.2.3203, 3388, 3400, 3871-3873, 3958, 4842, Singapore.

Oligodon taeniatus. - ZRC.2.4161, Bangkok, Thailand.

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A New *Philautus* (Amphibia: Rhacophoridae) from Northern Laos

BRYAN L. STUART[1,2,3,*] AND HAROLD F. HEATWOLE[4]

[1]*Field Museum of Natural History, Department of Zoology, Division of Amphibians & Reptiles, 1400 S. Lake Shore Drive, Chicago, Illinois, USA 60605-2496;*

[*]*Corresponding author: E-mail: bstuart@fieldmuseum.org*

[2]*University of Illinois at Chicago, Department of Biological Sciences, 845 W. Taylor, Chicago, Illinois, USA 60607-7060*

[3]*Wildlife Conservation Society, P.O. Box 6712, Vientiane, Laos*

[4]*North Carolina State University, Department of Zoology, P.O. Box 7617, Raleigh, North Carolina, USA 27695-7617; E-mail: harold_heatwole@ncsu.edu*

Abstract. - A new *Philautus* is described from Phou Dendin National Biodiversity Conservation Area in northern Laos. *Philautus petilus* sp. nov. is most remarkable by having a very slender, elongate habitus. Other distinguishing characteristics include having a tympanum diameter 80% of the eye diameter, white asperities on the dorsum, and distinctive coloration consisting of a soft yellow-beige dorsolateral surface with broken black stripes posteriorly, a lavender wash on dorsal surface of limbs, upper lip, and sides, a black stripe below edge of canthus extending from snout tip to flanks near level of mid-body, and a black spot equal in diameter to the tympanum located just anterior to the inguinal region.

Key words. - Laos, new species, *Philautus*, Rhacophoridae.

Introduction

Bourret (1942) remains the major work on the amphibians of Laos, supplemented only recently by descriptions of new species (Inger and Kottelat 1998; Stuart and Papenfuss 2002). Consequently, the amphibian fauna of Laos is imperfectly known.

From 6-26 October 1999, we conducted a herpetofaunal survey of Phou Dendin National Biodiversity Conservation Area in eastern Phongsaly Province, northern Laos, near to the tri-border area of Laos, Vietnam, and China (Figure 1A). The area surveyed was mostly covered in hilly evergreen forest, sometimes mixed with stands of natural bamboo, with small, rocky streams flowing down hillsides into the larger, swift Nam Ou and Nam Khang Rivers, at elevations from 600-1000 m. During the course of that work we found a single, adult female specimen of an enigmatic, rhacophorid treefrog, which we describe here as a new species of *Philautus*.

Materials and Methods

The single specimen found was caught in the field by hand, preserved in 10% buffered formalin, and later transferred to 70% ethanol. A tissue sample was taken by preserving pieces of liver in 95% ethanol before the specimen was fixed in formalin. The specimen was deposited at the Field Museum of Natural History (FMNH).

Measurements largely follow those of Bain et al. (2003) and were made with dial calipers to the nearest 0.1 mm. Abbreviations used are: SVL = snout-vent length; HDL = head length from tip of snout to the commisure of the jaws; HDW = head width at the commisure of the jaws; SNT = snout length from tip of snout to the anterior corner of the eye; EYE = eye diameter; IOD = interorbital distance; TMP = horizontal diameter of tympanum; TEY = tympanum-eye distance from anterior edge of tympanum to posterior corner of the eye; FPL = length of finger III disk from the base of the pad to its tip; FPW = width of finger III disc at the widest part of the pad; TPL = length of toe IV disk; TPW = width of toe IV disk. Measurement ratios are reported as percentages (%) rounded to the nearest integer.

Philautus petilus, new species
(Figure 1B)

Material examined. -Holotype: FMNH 257902, adult female, collected by the authors on 23 October 1999 in Phou Dendin National Biodiversity Conservation Area, Phongsaly District, Phongsaly Province, Laos, 22°05'44"N 102°08'10"E, at 600 m elevation.

Diagnosis. - An elongate, slender *Philautus* having a head width only 27% of SVL; tympanum diameter 80%

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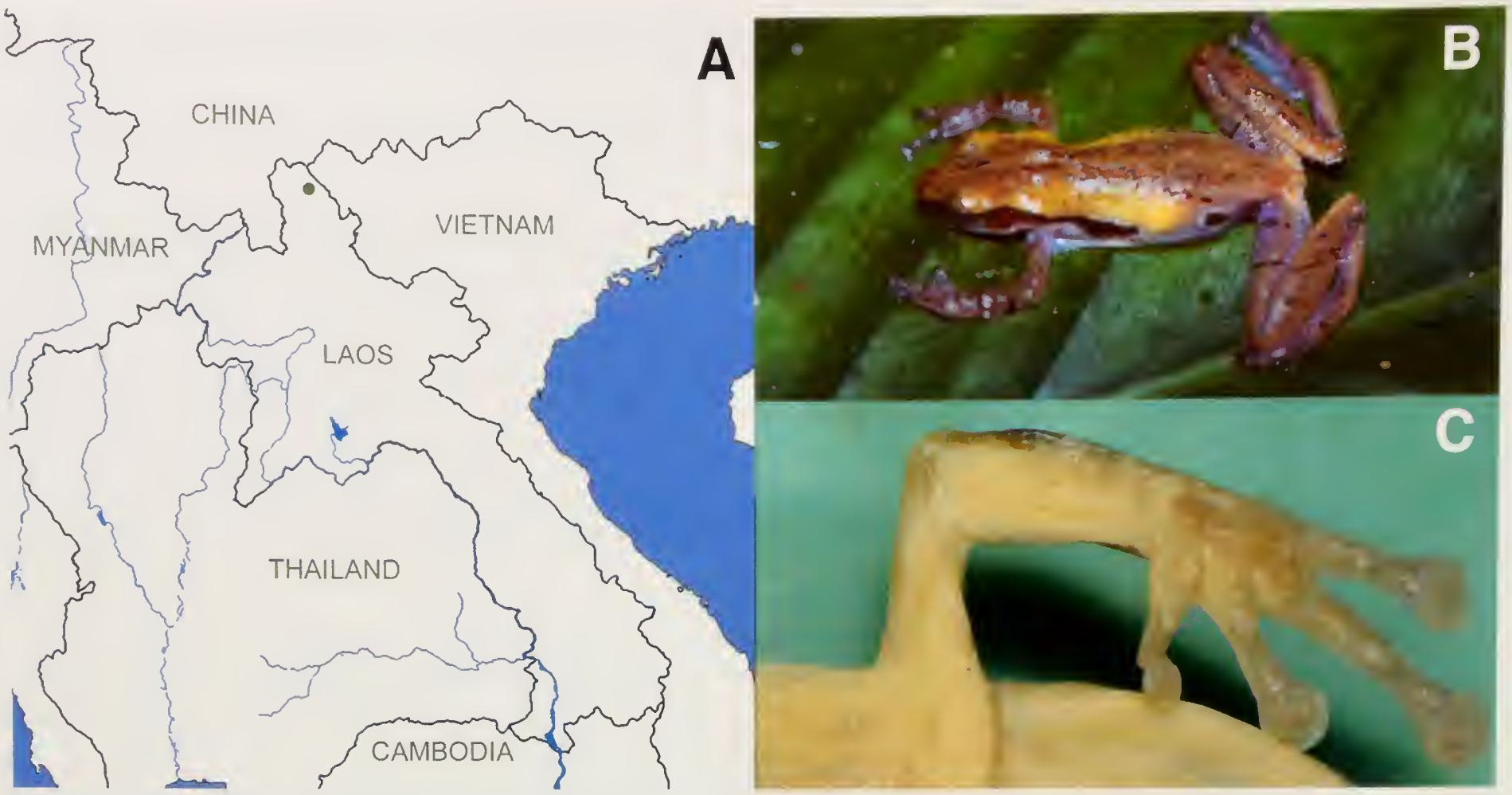

Figure 1A-C. A. Map showing the type locality (black dot) of *Philautus petilus* sp. nov. in Phongsaly Province, northern Laos. B. The adult female holotype (FMNH 257902) of *Philautus petilus* sp. nov., anesthetized prior to preservation. Photograph by Bryan L. Stuart. C. The hand of the adult female holotype (FMNH 257902) of *Philautus petilus* sp. nov. in preservation. Photograph by Nikolai L. Orlov.

of eye diameter; white asperities on head, eyelids, back, dorsal surface of tibia and forelimbs, and anterior half of sides; no fringes, row of enlarged tubercles, or accessory flaps of skin on outer margins of limbs; black stripe below edge of canthus extending from tip of snout to flanks near level of mid-body; black spot slightly anterior to inguinal region, equal in diameter to the tympanum.

Description of Holotype. - Habitus elongate, slender; head width 27% of SVL; head slightly longer than wide; snout obtusely pointed in dorsal view, projecting beyond lower jaw, round in profile, not depressed; nostril lateral, near tip of snout; canthus rounded but distinct, constricted behind nostrils; lores slightly concave, oblique; eye diameter less than snout length, interorbital distance wider than upper eyelid; tympanum visible, not depressed relative to skin of temporal region, tympanic rim slightly elevated relative to tympanum, tympanum diameter 80% of eye diameter; weak supratympanic fold from eye to shoulder; vomerine teeth very small, in oblique rows closer to choanae than to each other; tongue deeply notched posteriorly.

Tips of all four fingers expanded, about two times the width of phalanges, with circummarginal grooves, width of finger I disc 60% the width of finger III disc, width of finger III disc 71% the diameter of tympanum; relative finger lengths I < II < IV < III; webbing absent; fingers III and IV with large middle subarticular tubercle and smaller palmar tubercle at base; fingers I and II with large palmar tubercle at base.

Tips of toes expanded, width of toe IV disc slightly smaller than width of finger III disc; toe V longer than toe III; toe I webbing to midway between subarticular tubercle and disc, continuing only as narrow fringe to disc; toes II, III, and IV webbing to distal subarticular tubercle, continuing only as narrow fringe to disc; toe V webbing to midway between distal subarticular tubercle and base of disc, continuing only as narrow fringe to base of disc; inner metatarsal tubercle elongated, outer metatarsal tubercle very small, almost inconspicuous.

Skin on dorsal and ventral surfaces smooth, except for distinct, white asperities on head, eyelids, back, dorsal surface of tibia and forelimbs, and anterior half of sides; no fringes, row of enlarged tubercles, or accessory flaps of skin on outer margins of limbs.

Left ovary with fewer than 25, developing, creamy-white ova (color in preservative).

In life, top of head and back light brown with dark brown reticulations and scattered black spotting; dorsolateral surface of head and body soft yellow-beige, with short, broken black stripe on dorsolateral surface from level of midbody extending toward groin; lavender wash on dorsal surface of limbs, upper lip, and sides; black stripe below edge of canthus extending from tip of snout to anterior border of eye, and from posterior border of eye along supratympanic fold to flanks near level of mid-body; black spot slightly anterior to inguinal region,

equal in diameter to the tympanum; black 'M'-shaped marking over anus; black spot on tarsus closer to articulation than foot, narrow black crossbars on hindlimbs, some black flecking on forelimbs; venter creamy-white, dark spotting on chin and throat, pigmentation on underside of hands, feet, and tibiotarsus. In preservative, yellow-beige and lavender coloration lost.

Measurements (mm) of holotype. - SVL 33.8; HDL 9.9; HDW 9.2; SNT 4.1; EYE 3.0; IOD 2.3; TMP 2.4; TEY 1.5; FPL 1.5; FPW 1.7; TPL 1.3; TPW 1.4.

Comparisons. - The generic assignments of small, rhacophorid (or rhacophorine) treefrogs are uncertain and debated (Bossuyt & Dubois 2001; Wilkinson et al. 2002). Therefore, we compare *P. petilus* with all other species of small to medium-sized rhacophorid (or rhacophorine) treefrogs having reduced finger webbing that are reported from the vicinity of northern Laos, regardless of what genus they are currently referred to. These include *Chirixalus doriae* Boulenger, *C. hansenae* (Cochran), *C. laevis* (Smith), *C. nongkhorensis* (Cochran), *C. palpebralis* (Smith), *C. vittatus* (Boulenger), *Philautus abditus* Inger, Orlov, & Darevsky, *P. albopunctatus* Liu & Hu, *P. banaensis* Bourret, *P. carinensis* (Boulenger), *P. gracilipes* Bourret, *P. gryllus* Smith, *P. jinxiuensis* Hu, *P. longchuanensis* Yang & Li, *P. maosonensis* Bourret, *P. menglaensis* Kou, *P. ocellatus* Liu and Hu, *P. odontotarsus* Ye and Fei, *P. parvulus* (Boulenger), *P. rhododiscus* Liu and Hu, *Rhacophorus appendiculatus* (Günther), *R. baliogaster* Inger, Orlov & Darevsky, *R. bisacculus* Taylor, *R. verrucosus* Boulenger, *Theloderma asperum* (Boulenger), and *T. stellatum* Taylor (Bourret 1942; Taylor 1962; Inger et al. 1999; Fei 1999; Orlov et al. 2002).

Philautus petilus differs from all species of *Chirixalus* Boulenger by lacking the two outer fingers appearing to be opposable to the two inner ones (present in *Chirixalus*). *Philautus petilus* further differs from *C. doriae* and *C. nongkhorensis* by lacking outer finger webbing (outer fingers 1/3 webbed in *doriae* and *nongkhorensis*), from *C. hansenae*, *C. laevis* and *C. vittatus* by lacking light-colored dorsolateral stripes (present in *hansenae*, *laevis* and *vittatus*), and from *C. palpebralis* by lacking a yellow streak from below eye to shoulder (present in *palpebralis*). *Philautus petilus* differs from *P. abditus* by having a visible tympanum (hidden in *abditus*) and lacking large black spots on the legs (present in *abditus*). *Philautus petilus* differs from *P. albopunctatus* by having dorsal asperities (absent in *albopunctatus*) and lacking white blotches on the snout, dorsum and above anus (present in *albopunctatus*). *Philautus petilus* differs from *P. carinensis* by having the snout longer than the eye diameter (snout shorter than eye diameter in *carinensis*) and by having a slender habitus (stocky habitus in *carinensis*). *Philautus petilus* differs from *P. gracilipes* by having a head width 27% of SVL (head width 45% of SVL in *gracilipes*), having the width of finger III disc 71% the diameter of tympanum (width of finger III disc equal to the diameter of tympanum in *gracilipes*), and lacking mostly green coloration with dark-brown eyelids (present in *gracilipes*). *Philautus petilus* differs from *P. jinxiuensis* by lacking a large interorbital dark blotch extending posteriorly into two broad, dark dorsolateral stripes (present in *jinxiuensis*). *Philautus petilus* differs from *P. longchuanensis* by having a tympanum diameter larger than width of finger III disc (tympanum diameter smaller than width of finger III disc in *longchuanensis*). *Philautus petilus* differs from *P. maosonensis* by having the head slightly longer than wide (head wider than long in *maosonensis*), by having the snout projecting beyond the lower jaw (snout not projecting beyond lower jaw in *maosonensis*), by having the tympanum diameter 80% of eye diameter (tympanum diameter approximately 2/3 eye diameter in *maosonensis*), and by lacking a thin band between the eyelids, a large dark marking on the back, and a dark spot behind the axilla (present in *maosonensis*). *Philautus petilus* differs from *P. menglaensis* by having smooth skin with asperities on the dorsum (warty skin on dorsum in *menglaensis*) and by having a tympanum diameter larger than the width of finger III disc (tympanum diameter smaller than or equal to width of finger III disc in *menglaensis*). *Philautus petilus* differs from *P. ocellatus* by lacking a round black blotch on the occiput (present in *ocellatus*). *Philautus petilus* differs from *P. parvulus* by having the snout longer than the eye diameter (snout shorter than eye diameter in *parvulus*), having a visible tympanum (hidden in *parvulus*), and having the nostril close to the tip of snout (nostril midway between eye and tip of snout in *parvulus*). *Philautus petilus* differs from *P. rhododiscus* by lacking dark brown coloration with black spots, grayish-white ventral marbling, and reddish-orange finger and toe discs (present in *rhododiscus*). *Philautus petilus* differs from *P. banaensis*, *P. gryllus*, *P. odontotarsus*, *R. appendiculatus*, *R. bisacculus*, and *R. verrucosus* by lacking dermal fringes or tubercles on the limbs (present in *banaensis*, *gryllus*, *odontotarsus*, *appendiculatus*, *bisacculus*, and *verrucosus*). *Philautus petilus* differs from all species of *Theloderma* Tschudi by having smooth skin with dorsal asperities (skin rugose in *Theloderma*).

Etymology. - The species name *petilus* (L.) means slender, referring to the distinct habitus of the holotype.

Ecology. - The holotype was collected at 2215 h on a bamboo leaf 1 m above the ground in hilly evergreen

forest mixed with bamboo, approximately 200 m from the bank of the Nam Ou River, at 600 m elevation.

Remarks. - The generic assignments of small, rhacophorid (or rhacophorine) treefrogs are uncertain, debated, and likely to be considerably revised in the near future (Bossuyt & Dubois 2001; Wilkinson et al. 2002). Many species have been moved among the genera *Chirixalus* Boulenger and *Philautus* Gistel (Frost 2002). *Philautus petilus* does not have the two outer fingers appearing to be opposable to the two inner ones (Figure 1C), which is diagnostic of the genus *Chirixalus* (Liem 1970). Historically, *Philautus* was diagnosed by the absence of vomerine teeth (Leim 1970; Bossuyt and Dubois 2001), but this character is known to vary within a species, and consequently Liem (1970) included species in the genus *Philautus* that sometimes have vomerine teeth. *Philautus petilus* has very small vomerine teeth. Bossuyt and Dubois (2001) proposed that only species having direct aerial development (lacking a free-swimming aquatic tadpole) be included in the genus *Philautus*. The mode of reproduction in *P. petilus* is unknown, but it does have a small clutch size (the left ovary of the holotype holds fewer than 25 ova). Dring (1987) reported total clutch sizes of only 2-26 eggs in five species of *Philautus*, including the type species, *P. aurifasciatus*. In the absence of a phylogeny and more substantial reproductive data, we recognize that our placement of *petilus* into the genus *Philautus* is tentative.

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Rediscovery of the Philippine Forest Turtle, *Heosemys leytensis* (Chelonia; Bataguridae), from Palawan Island, Philippines

ARVIN C. DIESMOS[1,2,3], GENEVIEVE V. A. GEE[3], MAE L. DIESMOS[3, 4], RAFE M. BROWN[2,3,5], PETER J. WIDMANN[3,6], AND JUDELINE C. DIMALIBOT[7]

[1]*National Museum of the Philippines, Padre Burgos Avenue, Ermita 1000, Manila, Philippines; Current address: Department of Biological Sciences, National University of Singapore, Block S3 14 Science, Drive 4, Singapore 117543; E-mail: kaloula@i-manila.com.ph*

[2]*Angelo King Center for Research and Environment Management; Marine Laboratory, Silliman University, Bantayan, Dumaguete City, Negros Oriental, Philippines 6200.*

[3]*Wildlife Conservation Society of the Philippines, Room 106 Institute of Biology, University of the Philippines, Diliman 1101, Quezon City, Philippines; E-mail: jutisha@yahoo.com*

[4]*Department of Biological Sciences, College of Science, University of Santo Tomas España, Manila; E-mail: msleonida@lycos.com*

[5]*Section of Integrative Biology, University of Texas, Austin Texas, 78712; Current address: Museum of Vertebrate Zoology, 3101 Valley Life Science Building, University of California, Berkeley, CA 94720; Email: rafe@mail.utexas.edu*

[6]*KATALA Foundation, Jacana Road, Bancao-Bancao, P.O. Box 390, Puerto Princesa City 5300, Palawan, Philippines; E-mail: widpeter@yahoo.com*

[7]*Palawan Council for Sustainable Development, Sta Monica, Puerto Princesa City 5300, Palawan, Philippines.*

Abstract. - We report new observations from natural populations of the critically endangered Philippine forest turtle, *Heosemys leytensis*. Previously known from two cotypes (reportedly from Leyte Island) that were destroyed during World War II, a lone specimen in a U.S. collection, and a specimen purchased on Palawan Island in the late 1980s, its status in the wild has been uncertain since its discovery. Our recent surveys of Palawan and nearby Dumaran islands have documented natural populations that are under immediate threat due to over-harvesting and loss of habitat. Records of captive animals and interviews with residents from these islands suggest that this species is heavily exploited for food, pet trade, and ornamental fish pond curiosities. There is an urgent need to establish a conservation program to study and protect remaining natural populations.

Key words. - *Heosemys leytensis*, Asian freshwater turtles, turtle trade, Philippine forest turtle, Palawan Island, Philippines.

Introduction

Taylor (1920) described the Philippine forest turtle, *Heosemys leytensis*, on the basis of two specimens that were collected by Gregorio Lopez. These specimens were reportedly collected from a swamp at the Municipality of Cabalian, southern Leyte Province, Leyte Island, Philippines (Fig. 1). The cotypes (a male and a female) were eventually deposited in the Philippine Bureau of Science (Taylor, 1944) but were destroyed during the World War II firebombing of Manila (Brown and Alcala, 1978; Buskirk, 1989).

Between Taylor's (1920) description and the late 1980s, no additional specimens or information became available for this species, although its status as a valid species has never been challenged (e.g., Pritchard, 1979; Ernst and Barbour, 1989; Iverson, 1992). In 1988, Timmerman and Auth reported on a specimen purchased from a local resident of the Municipality of Taytay, northern Palawan Island (Fig. 1). Buskirk (1989) described a neotype for the species (CAS 60930) based on a single specimen also reportedly from Cabalian, Leyte.

Since these reports, numerous herpetologists, including us, have searched for *H. leytensis* at Cabalian, Leyte (Fig. 1) without success. The apparent rarity of the species formed the basis of its listing under CITES Appendix II and by IUCN as a Critically Endangered species (Hilton-Taylor, 2000). Chelonian biologists questioned whether the species was really rare or just unstudied, extinct or extirpated, and whether the specimen reported by Timmerman and Auth (1988) was from

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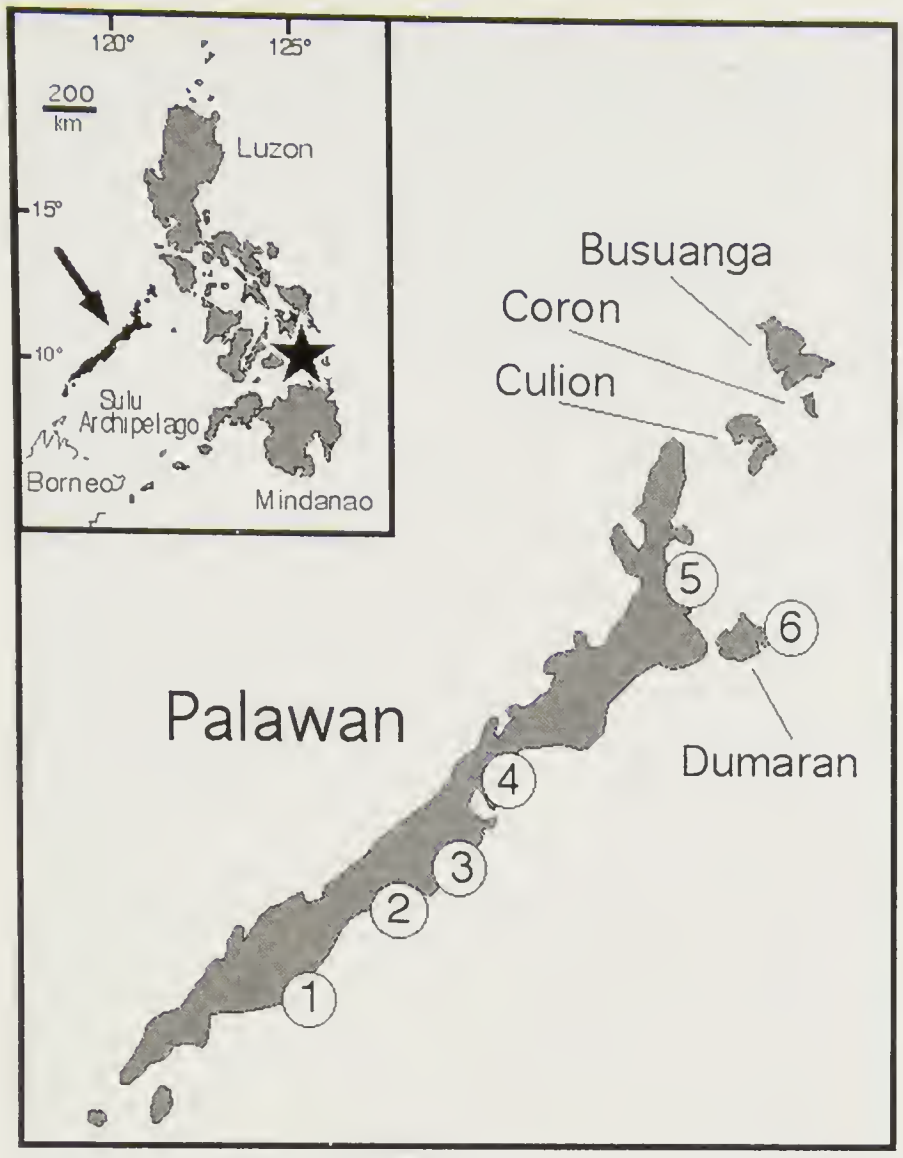

Figure 1. - Map of Palawan Island group in relation to the Philippines (inset) and Leyte Island. The type locality (Taylor, 1920) of *H. leytensis* is indicated with a star; recent trade or captive animal locations include (1) Brooke's Point, (2) Rizal, (3) Aborlan, and (4) Puerto Princesa and known natural populations include (5) Taytay, and (6) Dumaran Island.

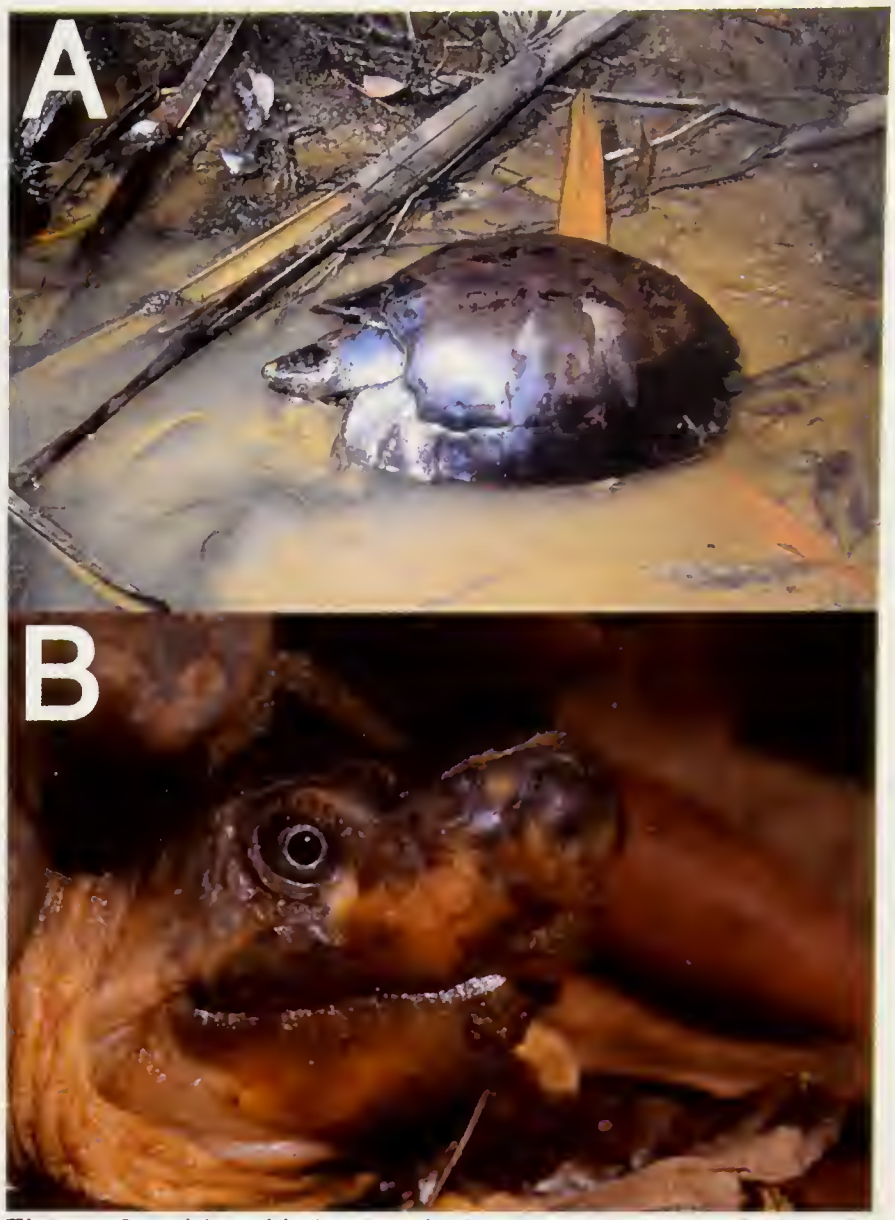

Figure 2. - Live *H. leytensis* from natural population on Dumaran Island, northern Palawan: (A) An individual of undetermined sex in a small stream on Dumaran Island; (B) close up of the head.

a natural population on Palawan or the result of interisland trade (Ernst and Barbour, 1989; Iverson, 1992; Das, 1995; Gaulke, 1995). The question remained whether *H. leytensis* occurred on Leyte Island or whether the original type locality data were in error.

In late 2001, as part of a comprehensive status assessment of Palawan's endemic amphibians and reptiles, we began a survey of forested sites throughout the island. We soon became aware of three nonmarine turtle species present in some local wet markets and in the possession of local wildlife traders. Two species *Cuora amboinensis* and *Cyclemys dentata*, are common on Palawan (Taylor, 1920; Alcala, 1986; Gaulke and Fritz, 1998; Widmann, 1998; ACD and RMB, pers. obs.). A third species, frequent in the wildlife and food trade, was identified as Taylor's (1920) *Heosemys leytensis*.

New observations. - The live specimens we examined match published descriptions of *H. leytensis* (Taylor, 1920; Buskirk, 1989; Ernst and Barbour, 1989): carapace unkeeled except for posterior vertebrals; vertebrals broader than long; anterior marginals projecting beyond cervicals, rendering anterior rim from slightly to strongly serrated; plastron much smaller than carapace, narrowing anteriorly and posteriorly; angular notch between gulars deep and distinct; notch between gulars and humerals present, less distinct; anal notch deep and circular; three to four enlarged transverse scales present on anterior side of each foreleg; coloration rusty brown with darker margins on anterior scutes; narrow white to pale yellow line crosses head just behind auricular openings, medially divided in some specimens (Figs. 2-5). A full technical redescription of the morphology of *H. leytensis* will be published elsewhere (Diesmos et al., unpublished data).

We located captive animals for sale in markets at the Municipalities of Brookes Point, Aborlan, Rizal, Puerto Princesa City, and Taytay (Fig. 1). The animals were for sale as pets, ornamental fish pond curiosities, and for food. Additionally, *H. leytensis* individuals were found in public restaurants in the capital city of Puerto Princesa (Fig. 4b). In many areas, residents expressed the belief that the keeping of pet *H. leytensis* specimens brings the owner good luck.

We found natural populations in the vicinity of Lake Manguao, Municipality of Taytay, Palawan Island and on Dumaran Island (Fig. 2). Exact localities are not given to protect these populations. Several individuals of each natural population were observed in slow-mov-

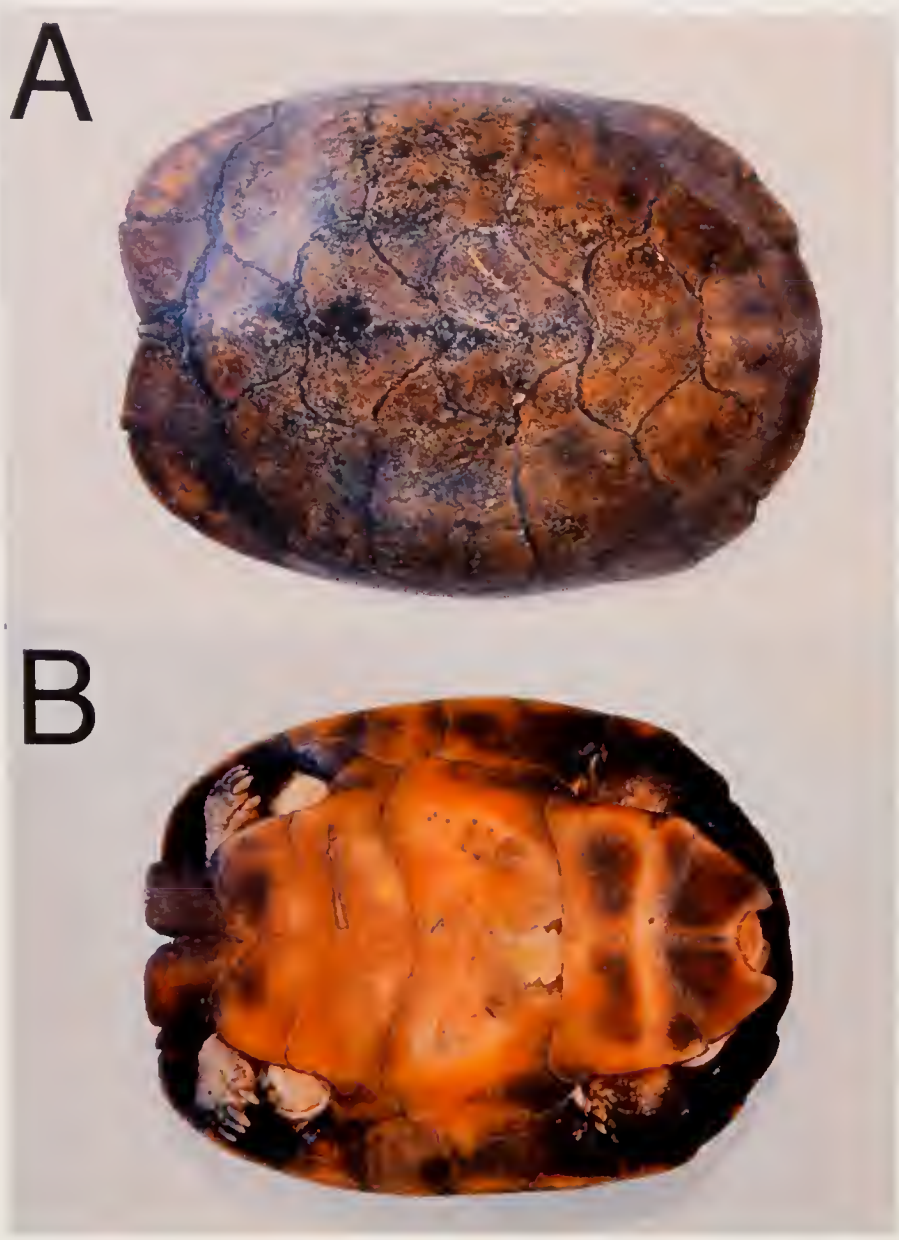

Figure 3. - (A) Dorsal view of carapace and (B) ventral view of plastron of a subadult *H. leytensis* of undetermined sex (captive pet, reportedly wild-caught locally) from Dumaran Island, N. Palawan.

Figure 4. - (A) Preferred stream habitat of *H. leytensis* from Dumaran Island, northern Palawan; (B) *Heosemys leytensis*, *Cuora amboinensis*, and *Cyclemys dentata* specimens alive in captivity in restaurant of Puerto Princesa City, Palawan Island.

ing streams, quiet side pools, and nearby disturbed gallery forests (Fig. 4a), at most a few meters from the water's edge. Residents in these localities reported to us that turtles are always located in the general vicinity of water, but that they can be found many meters away from water as well. Residents also report that *H. leytensis* burrows in stream banks and retreats under large nearby limestone boulders in the dry season when streambeds run dry.

Interviews with Tagbanwa tribe members in the Municipality of Taytay suggest that in some areas this species is fairly common. Reports of natural populations in the southern localities of Rizal and Brookes Point will need to be confirmed. In these areas interviewed persons claimed that *H. leytensis* was present in nearby forests but we were unable to locate wild animals ourselves.

Discussion

Our recent field observations confirm that *H. leytensis* occurs naturally on Palawan and at least on one of its northern satellite islands. Despite numerous surveys of suitable habitat at Cabalian, Leyte conducted by E. Taylor, A. Alcala, and ourselves, no additional specimens of *H. leytensis* have been collected there. Interviews with residents in the vicinity of Cabalian, have failed to find verbal accounts of fresh-water turtles that fit the description of *H. leytensis*. We suspect that the species does not and never has naturally occurred on Leyte. We prefer the use of the common name "Philippine forest turtle" given that we have only observed animals in remnant old-growth forests and our sense is that this species is forest dependent.

It is possible that Taylor or Lopez mislabeled or otherwise confused locality information assigned to the original co-types on Leyte and the third specimen at CAS (Buskirk, 1989). Taylor (1920) also reported *Cyclemys dentata* from Cabalian, Leyte (see also Iverson, 1992). This species has not since been reported from Leyte and is otherwise restricted in the Philippines to Palawan and the Sulu archipelago (Fig. 1; Taylor, 1920; Gaulke, 1995; Gaulke and Fritz, 1998). The fact that another conspicuous Palawan turtle species was reported at the same time and from the same site on Leyte (Taylor, 1920) suggests that a group of specimens from Palawan were mixed into collections from Leyte or

Figure 5. - A live *Heosemys leytensis* from the Municipality of Taytay, northern Palawan Island, Philippines. Watercolors by Mr. Rene Aquino.

were mislabeled. Based on information from the CAS herpetological registry, it is clear that G. Lopez also collected on Coron and Busuanga (Fig. 1) which would appear to be a likely source of the presumably erroneous "Leyte" specimens of *C. dentata* and *H. leytensis*. Thus, we suspect that a locality error is the basis of the specific epithet and the long-held belief that *H. leytensis* naturally inhabits the island of Leyte. Whether *H. leytensis* has ever been introduced outside of Palawan or the country, remains to be documented.

Finally, given the geological history and the Pleistocene formation of isolated paleoislands in the Philippines (Heaney, 1985; Hall, 1996, 1998) it is not surprising that *H. leytensis* may be restricted to Palawan and satellite islands. Based on available information from other groups of Philippine endemics, it is somewhat rare for a species to be shared between both the Palawan (Palawan + Busuanga + Coron + Culion + Dumaran) and the Mindanao (Mindanao+Bohol+Leyte+ Samar) Pleistocene Aggregate Island Complexes (PAICs). That is, based on previously-elucidated patterns of biogeography (Brown and Alcala, 1970; Brown and Diesmos, 2001; Brown and Guttman, 2002; Evans et al., 2003), we would expect to find Philippine endemics with restricted distributions on the Palawan PAIC or the Mindanao PAIC, but not necessarily both. There are some exceptions to these apparent trends, but they appear to be rare and limited to non-endemic widespread species that are also shared with the islands of the Sunda Shelf (Borneo, Java, Sumatra, etc.), or widespread Philippine endemics that are also found throughout the rest of the archipelago (Inger, 1954; Alcala and Brown, 1998; Brown and Alcala, 1970, 1978, 1980)

Recommendations. - We recommend that an immediate exhaustive survey of the Palawan PAIC (including Balabac, Coron, Busuanga, Culion, and Dumaran) be undertaken to determine the status of natural *H. leytensis* populations. Basic knowledge of the species' distribution, habitat requirements, and natural population size will be a necessary requirement for designing effective conservation strategies. To combat illegal hobbyist, consumptive, and/or medicinal trade, wildlife managers will need to have reasonable estimates of numbers of animals

Table 1. - Standard measurements of *H. leytensis* specimens from captivity (Nos. 1-20) and a natural population (Nos. 21-24; Dumaran Isl.). Carapace Length and Width are straight-line distances; Carapace Width measured at widest point; Tail Length measured from posterior edge of cloaca to tip of tail. Sex undetermined; all measurements are in mm.

Number	Carapace Length	Carapace Width	Plastron Length	Tail Length
1.	177.0	134.3	153.8	15.9
2.	183.8	139.6	151.6	17.6
3.	189.6	144.5	157.2	19.8
4.	192.5	142.4	158.1	18.3
5.	192.7	148.4	150.8	19.1
6.	196.4	152.2	151.4	20.4
7.	200.1	148.1	165.9	22.2
8.	203.6	151.8	171.4	19.2
9.	210.2	157.3	118.1	35.6
10.	215.9	160.8	179.7	19.9
11.	222.3	171.2	186.6	35.1
12.	231.2	172.2	185.2	22.8
13.	248.5	191.5	206.8	18.6
14.	261.7	191.0	210.3	25.5
15.	266.3	195.5	201.5	26.2
16.	269.9	196.4	213.0	23.4
17.	271.7	198.3	206.7	21.7
18.	275.3	200.5	205.6	19.7
19.	278.0	200.4	208.9	27.1
20.	280.0	201.6	205.2	29.1
21.	290.6	207.8	216.3	27.7
22.	297.8	211.4	208.5	30.9
23.	299.6	212.4	212.1	28.2
24.	299.9	212.9	213.0	35.0

being illegally harvested. Legislative protection of the species will need to be adjusted to recognize its current known distribution on Palawan and not Leyte. We expect that a specific conservation strategy will be necessary to protect this species from unchecked exploitation. The fact that the entirety of Palawan is officially designated a national protected area provides some assurance, but we suspect additional measures will need to be undertaken to protect this species while promoting its study. The legal "Protected Area" status of Palawan Island clearly is not deterring local exploitation of this species. Local education programs and public awareness campaigns targeting both the general public and local environmental authorities may be the key to insuring that *H. leytensis* does not become another casualty of the "Asian turtle crisis" (van Dijk et al., 2000). Many basic questions regarding the distribution, demography, ecology, reproductive biology, and phylogenetic affinities of *H. leytensis* remain to be answered.

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Molecular Systematics of Old World Stripe-Necked Turtles (Testudines: *Mauremys*)

CHRIS R. FELDMAN[1,*] AND JAMES F. PARHAM[2,3]

[1]*Department of Biology, Utah State University, Logan, UT, 84322-5305, USA,*
** Corresponding Author E-mail: elgaria@biology.usu.edu.*
[2]*Evolutionary Genomics Department, Joint Genome Institute, 2800 Mitchell Drive, Walnut Creek, CA, 94598, USA.*
[3]*University of California Museum of Paleontology, University of California, Berkeley, CA, 94720-3140, USA, E-mail: parham@socrates.berkeley.edu*

Abstract. - Nine extant species of *Mauremys* (including *Ocadia* and *Chinemys*) represent a geographically widespread yet morphologically and ecologically conservative group of batagurid turtles. Here we examine the evolutionary relationships of *Mauremys* using 1539 base pairs of mitochondrial DNA encoding portions of COI, ND4, and three adjacent tRNA genes. These data contain 246 parsimony informative characters that we use to erect hypotheses of relationships for *Mauremys*. Both maximum parsimony and Bayesian methods suggest that *Mauremys japonica*, *M. sinensis*, *M. nigricans*, and *M. reevesii* form a well-supported monophyletic clade, as do *M. mutica* and *M. annamensis*. Furthermore, our analyses show that *M. mutica* is paraphyletic with respect to *M. annamensis*. The western taxa *M. leprosa*, *M. caspica*, and *M. rivulata* remain problematic and do not form a monophyletic group sister to the Asian taxa. Nevertheless, an east-west biogeographic hypothesis cannot be discounted with our molecular genetic data.

Key words. - Turtles, Bataguridae, *Mauremys*, molecular phylogenetics, mitochondrial DNA

Introduction

The Old World turtle genus *Mauremys* is represented by morphologically and ecologically conservative species that are diagnosed by a rigid plastron and a striped head and neck. These semi-aquatic, batagurid (= geoemydid, see Joyce et al., in press) turtles occupy lotic and lentic environments in both forested and arid habitats throughout Asia and the Mediterranean.

The genus contains some of the most commercially important freshwater turtles in Asia. For example, *M. mutica* is one of the most commonly reared and highly traded chelonians in Asia (Lau and Shi, 2000). Other *Mauremys* species have been at the center of a conservation and systematics controversy. In fact, two newly described *Mauremys* may be polyphyletic hybrids (Parham et al., 2001; Wink et al., 2001; Spinks et al., 2004).

Given the mounting conservation interest in the turtle fauna of Asia (van Dijk et al., 2000), understanding the extant diversity and phylogenetic relationships among the Bataguridae are areas of active research (Wu et al., 1999; Honda et al., 2002b; Barth et al., 2004; Spinks et al., 2004). The genus *Mauremys* has received particular attention because of this recent conservation crisis and taxonomic confusion. The first examination of evolutionary relationships within *Mauremys* was a morphological treatment of the genus based on shell and scute measurements (Iverson and McCord, 1994). Consistent with the disjunct distribution of *Mauremys*, Iverson and McCord (1994) suggested that East Asian taxa form a monophyletic group, sister to a Mediterranean and Middle Eastern clade. A subsequent study used 12S and 16S ribosomal genes to resolve the phylogenetic relationships among species of *Mauremys* (Honda et al., 2002a). In contrast to the east-west hypothesis of Iverson and McCord (1994), Honda et al. (2002a) suggested that the deepest phylogenetic splits within *Mauremys* occur between Asian taxa. The ribosomal mtDNA data also cast doubt on the monophyly of traditional *Mauremys* by including the east Asian species, *Chinemys reevesii*, as the sister taxon to *M. japonica*. Two recent studies examined more extensive sequence data, predominantly cyt *b* mtDNA, as well as a more comprehensive sampling of batagurids (Barth et al., 2004; Spinks et al., 2004). Both studies firmly established the placement of *Mauremys* within the Bataguridae and show that the *Chinemys* and *Ocadia* are phylogenetically nested within *Mauremys* (Barth et al., 2004; Spinks et al., 2004). Barth et al. (2004) offer two possible solutions to reconcile the paraphyly of *Mauremys*: 1) split the species of *Mauremys* into four genera; 2) lump *Chinemys* and *Ocadia* into an expanded *Mauremys*. While Barth et al. (2004) refrain from a taxonomic decision, Spinks et al. (2004) adopt an expanded *Mauremys*. We also endorse an inclusive *Mauremys*

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because we consider expanding genera to well-supported clades of species functionally preferable to proliferating monotypic genera based on subjective, typological ideas of uniqueness (Feldman and Parham, 2002; Parham and Feldman, 2002; Spinks et al., 2004).

Our objective here is to provide an independent estimate of *Mauremys* phylogeny using different molecular markers from other recent systematic investigations and separate museum voucher specimens (Barth et al., 2004; Spinks et al., 2004). We hope that our data help resolve areas of uncertainty in the emerging consensus on *Mauremys* systematics. In addition, our study will add to the growing body of information on the evolutionary history and diversity of Asia's threatened batagurid fauna (Wu et al., 1999; Honda et al., 2002b; Barth et al., 2004; Spinks et al., 2004).

Materials and methods

Taxon sampling and laboratory protocols. - We obtained liver tissue from 17 museum specimens representing nine currently recognized species of *Mauremys* and three species of *Cuora* (Appendix 1). The nine species of *Mauremys* used in our study include: *M. annamensis*, *M. caspica*, *M. japonica*, *M. leprosa*, *M. mutica*, *M. nigricans*, *M. reevesii*, *M. rivulata*, and *M. sinensis*. We do not consider "*M. iversoni*", "*M. pritchardi*", "*O. glyphistoma*" or "*O. philippeni*" to be valid taxa because specimens matching these species (all described from the pet trade) are likely hybrids (Parham et al., 2001; Wink et al., 2001; Spinks et al., 2004). In addition, we also excluded "*M. megalocephala*", which is probably a diet-induced variant of *M. reevesii* (Iverson et al., 1989; Barth et al., 2002). However, we do include a "*M. iversoni*"-like hybrid specimen described in Parham and Shi (2001) because mtDNA from this hybrid specimen is demonstrably *Mauremys* (Parham et al., 2001). All vouchers correspond to well-documented reference material and original species descriptions.

We isolated genomic DNA from tissue samples by standard proteinase K digestion and phenol/chloroform purification (Maniatis et al., 1982). We amplified 700 bp of mtDNA encoding a section of COI via PCR (Saiki et al., 1988) using primers HCO-2193 and LCO-1490 (Folmer et al., 1994). We amplified an additional 900 bp region of mtDNA encoding a portion of ND4 and flanking tRNA histidine ($tRNA^{his}$), serine ($tRNA^{ser}$), and part of leucine ($tRNA^{leu}$) using primers ND4 and Leu (Arevalo et al., 1994). We used the following thermal cycle parameters for 50µl amplification reactions: 35 cycles of 1min denature at 94°C, 1min anneal at 45°C (COI) or 52°C (ND4), and 2min extension at 72°C. We purified PCR products using the Wizard Prep Mini Column Purification Kit (Promega, Inc.) and used purified template in 10µl dideoxy chain-termination reactions (Sanger et al., 1977) using ABI Big Dye chemistry (Applied Biosystems, Inc.) and the primers listed above. Following an isopropanol/ethanol precipitation, we ran cycle-sequenced products on a 4.8% Page Plus (Ameresco) acrylamide gel using an ABI 377 automated sequencer (Applied Biosystems, Inc.). We sequenced all samples in both directions.

Sequence analyses. - We aligned DNA sequences with the program Sequencher™ 4.1 (Gene Codes Corp.), and translated protein coding nucleotide sequences into amino acid sequences using MacClade 4.0 (Maddison and Maddison, 2000). We identified tRNA genes by manually reconstructing their secondary structures using the criteria of Kumazawa and Nishida (1993). We deposited all mitochondrial DNA sequences in GenBank (Appendix 1).

We performed a partition homogeneity test (PH), similar to the incongruence length differences test (ILD; Farris et al., 1994), to determine whether the ND4 and COI data could be combined. We used PAUP* 4.0b10 (Swofford, 2002) to generate a null distribution of length differences using 1000 same-sized, randomly generated partitions from the original data with replacement.

To evaluate base substitution saturation at first, second, and third codon positions, we plotted the uncorrected percent sequence divergence of transitions and transversions versus the corrected maximum likelihood estimates of divergence for each codon position.

Phylogenetic analyses. - We used maximum parsimony (MP; Farris, 1983) and maximum likelihood-based Bayesian (Larget and Simon, 1999) phylogenetic methods to infer evolutionary relationships among batagurid species. We conducted MP analyses in PAUP* and Bayesian analyses with MrBayes 3.0b4 (Huelsenbeck and Ronquist, 2001). We polarized the phylogeny via outgroup comparison (Maddison et al., 1984) using the Asian box turtles *Cuora mouhotii*, *Cuora picturata*, and *Cuora trifasciata*. Other molecular phylogenetic studies suggest these turtles are appropriate outgroup taxa (Wu et al., 1999; Honda et al., 2002b; Barth et al., 2004; Spinks et al., 2004).

We executed MP analyses with the branch-and-bound search algorithm (Hendy and Penny, 1982) using equally weighted, unordered characters. To assess nodal support, we used the bootstrap resampling method (BP; Felsenstein, 1985) employing 1000 pseudoreplicates of branch-and-bound searches in PAUP*. Additionally, we calculated branch support (DI; Bremer, 1994) for all nodes using the program Tree Rot 2c (Sorenson, 1999).

We performed Bayesian analyses to estimate branch lengths and search for additional tree topologies. To

determine the most appropriate model of DNA substitution for reconstructing *Mauremys* relationships under the Bayesian method, we executed hierarchical likelihood ratio tests (LRT; Felsenstein, 1993; Goldman, 1993; Yang, 1996) in the program Modeltest 3.06 (Posada and Crandall, 1998). Because MrBayes 3.0b4 can perform singular phylogenetic analyses using different models of evolution, we performed two separate LRTs on the two mtDNA regions. The model of nucleotide substitution that best fit the COI data was the HKY model (Hasegawa et al., 1985) in conjunction with Γ (Yang, 1994a; 1994b), and I (Gu et al., 1995), while the slightly less complex HKY + Γ model of DNA evolution best fit the ND4 data. We then performed Bayesian tree searches, allowing separate parameter estimates under the two models of DNA substitution for the COI and ND4 data partitions. We did not specify a topology or nucleotide substitution model parameters *a priori*. We ran Bayesian analyses for 3 x 10^6 generations using the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) algorithm with four heated Markov chains per generation, sampling trees every 100 generations. To determine when the Markov chains had converged on stable likelihood values, we plotted the -lnl scores against the number of generations (Huelsenbeck and Ronquist, 2001). We then computed a 50 % majority rule consensus tree after excluding those trees sampled prior to the stable equilibrium. Nodal support is given by the frequency of the recovered clade, which corresponds to the posterior probability of that clade under the given models of sequence evolution (PP; Rannala and Yang, 1996; Huelsenbeck and Ronquist, 2001). Lastly, we performed three Bayesian runs to be sure that independent analyses converged on similar log-likelihood scores (Leaché and Reeder, 2002).

Results

Genetic variation. - Sequences from the protein coding regions appear functional and there are no gene rearrangements in the data (Kumazawa and Nishida, 1995; Kumazawa et al., 1996; Macey and Verma, 1997; Macey et al., 1997). However, ND4 in the batagurids studied here appears truncated relative to that of emydid turtles, which have three additional residues: Phenylalanine, Tyrosine, and Cysteine (Feldman and Parham, 2002). Instead, these batagurids possess a stop codon, followed by a 12 bp stretch of highly polymorphic DNA between ND4 and $tRNA^{his}$. Additionally, $tRNA^{ser}$ has a short D-stem, instead of a D-arm replacement loop like that of most metazoan taxa (Kumazawa and Nishida, 1993). This unusual tRNA condition is also seen in emydid turtles (Feldman and Parham, 2002).

The PH test shows that length difference between the sum of the COI and ND4 trees and the combined COI and ND4 trees is not significantly different from the randomly generated test statistic ($P = 0.93$). Therefore, we combined the aligned DNA sequences for subsequent phylogenetic analyses.

Of the 1539 aligned nucleotides, 369 are variable and 246 are parsimony informative. Among ingroup taxa, 289 sites are variable and 205 parsimony informative. Of the 369 variable characters, 60 occur at 1st codon positions, 15 at 2nd positions, 261 at 3rd positions, and 33 in tRNAs. The scatter diagrams are linear and show no evidence of multiple hit problems for transitions or transversions (data not shown).

Phylogenetic relationships. - The branch-and-bound equally weighted MP analysis produces a single most parsimonious tree (L = 661; CI = 0.626; RI = 0.683) that is consistent with the model-based Bayesian analyses (Fig. 1). All three Bayesian analyses converge on the same topology and nearly identical mean log-likelihood values, parameter estimates, and nodal support. Thus we simply present results from the final search. The partitioned HKY + Γ + I and HKY + Γ Bayesian analysis (3 x 10^6 generations) attains stable log-likelihood values within the first 15,000 generations, but we were conservative and discarded the first 20,000 generations. Because we sampled trees every 100 generations, we discarded the first 200 trees and retained 29,800 Bayesian trees, which we used to generate a 50% majority rule tree, and for which consensus values represent a group's posterior probability (Huelsenbeck and Ronquist, 2001). The summary topology of the nearly 30,000 Bayesian trees (mean -lnl = 5205.5110, σ^2 = 24.5038; mean ti/tv (COI) = 10.8360; σ^2 = 10.6335; mean α(COI) = 0.5479, σ^2 = 0.8874; mean P_{invar}(COI) = 0.4163, σ^2 = 0.0291; mean ti/tv (ND4) = 12.3499; σ^2 = 9.0505; mean α(ND4) = 0.2431, σ^2 = 0.0009) differs from the MP tree in the placement of only one taxon (Fig. 1).

In both analyses, species of *Cuora* unambiguously group to the exclusion of *Mauremys*, (BP = 100%; DI = 19; PP = 100%). *Mauremys japonica* is a member of a clade containing *M. nigricans, M. reevesii* and *M. sinensis* (BP = 100%; DI = 13; PP = 100%), yet relationships among these taxa are not well resolved, as indicated by the low nodal support and conflict between MP and Bayesian reconstructions. The MP tree places *M. sinensis* sister to a group linking *M. japonica*, *M. nigricans*, and *M. reevesii* (DI = 1), wherein *M. nigricans* and *M. reevesii* form an additional clade (BP = 86%; DI = 5). Alternatively, the Bayesian tree connects *M. japonica* to *M. sinensis* (PP = 59%), sister to the *M. nigricans* the *M. reevesii* clade (PP = 99%). The *M. japonica*, *M. nigricans*, *M. reevesii*, and *M. sinensis* clade is sister to a

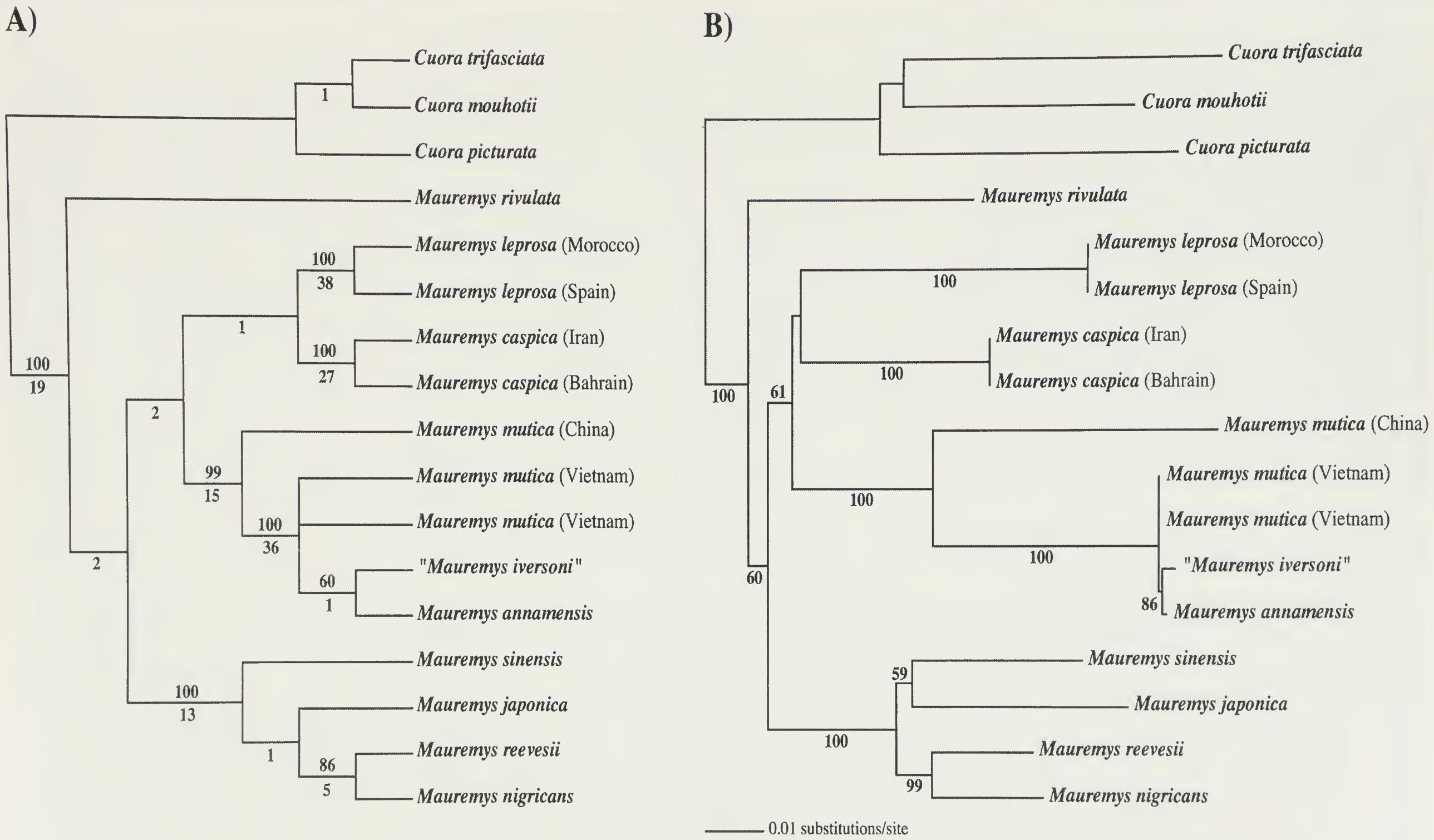

Figure 1. Phylogenetic trees for *Mauremys*. Country of origin given for species with multiple samples; hybrid taxon is in quotes. A) Single most parsimonious tree based on equally weighted characters (L = 661; CI = 0.626; RI = 0.683). Numbers above nodes indicate bootsrap support, those below nodes represent decay indices. B) Bayesian estimate of *Mauremys* phylogeny based on 29,800 trees built under partitioned HKY +Γ+ I and HKY +Γ models of DNA evolution (mean -lnl = 5205.5110, $\sigma^2 = 24.5038$; mean ti/tv (COI) = 10.8360; $\sigma^2 = 10.6335$; mean α(COI) = 0.5479, $\sigma^2 = 0.8874$; mean P_{invar} (COI) = 0.4163, $\sigma^2 = 0.0291$; mean ti/tv (ND4) = 12.3499; $\sigma^2 = 9.0505$; mean α(ND4) = 0.2431, $\sigma^2 = 0.0009$). Numbers along nodes represent posterior probability values. Branch lengths drawn proportional to Bayesian estimates of genetic divergence.

Table 1. Pairwise comparisons of mtDNA sequences among Mauremys and related taxa. Note: values above the diagonal indicate uncorrected pairwise differences (%) while those below the diagonal denote HKY + Γ + I sequence divergences (%).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 *M. nigricans*	-	3.12	7.74	5.66	5.66	7.74	5.07	6.31	6.31	8.26	7.61	7.61	6.18	4.16	8.65	8.71	8.58
2 *M. reevesii*	3.68	-	7.74	5.33	5.33	7.74	4.75	6.50	6.50	8.06	7.61	7.61	6.18	4.42	8.65	8.39	8.32
3 *M. annamensis*	11.72	11.72	-	6.89	6.89	0.26	8.65	7.67	7.67	6.31	0.13	0.13	6.83	8.32	8.97	9.30	9.62
4 *M. caspica* (Iran)	7.56	7.01	9.75	-	0	7.02	6.76	5.92	5.92	7.09	6.76	6.76	5.79	6.24	8.71	8.52	8.52
5 *M. caspica* (Bahrain)	7.56	7.01	9.75	0	-	7.02	6.76	5.92	5.92	7.09	6.76	6.76	5.79	6.24	8.71	8.52	8.52
6 "*M. iversoni*"	11.71	11.71	0.26	10.00	10.00	-	8.65	7.67	7.67	6.31	0.26	0.26	6.96	8.32	8.84	9.17	9.49
7 *M. japonica*	6.63	6.16	13.95	9.78	9.78	13.94	-	8.00	8.00	8.58	8.52	8.52	7.48	4.94	10.14	9.75	9.36
8 *M. leprosa* (Spain)	8.92	9.28	11.59	7.98	7.98	11.59	12.66	-	0	7.80	7.54	7.54	6.96	6.83	8.45	8.13	8.13
9 *M. leprosa* (Morocco)	8.92	9.28	11.59	7.98	7.98	11.59	12.66	0	-	7.80	7.54	7.54	6.96	6.83	8.45	8.13	8.13
10 *M. mutica* (China)	12.83	12.68	8.96	10.34	10.34	8.96	13.95	12.13	12.13	-	6.18	6.18	7.54	7.41	9.69	9.49	9.49
11 *M. mutica* (Vietnam)	11.45	11.44	0.13	9.51	9.51	0.26	13.64	11.32	11.32	8.72	-	0	6.70	8.19	8.84	9.17	9.49
12 *M. mutica* (Vietnam)	11.45	11.44	0.13	9.51	9.51	0.26	13.64	11.32	11.32	8.72	0	-	6.70	8.19	8.84	9.17	9.49
13 *M. rivulata*	8.57	8.65	9.86	7.75	7.75	10.11	11.37	10.15	10.15	11.30	9.61	9.61	-	6.05	8.32	8.00	8.32
14 *M. sinensis*	5.17	5.62	13.24	8.74	8.74	13.22	6.52	10.09	10.09	11.25	12.94	12.94	8.49	-	9.04	8.39	8.26
15 *Cuora picturata*	13.92	14.08	14.82	13.80	13.80	14.50	18.11	13.64	13.64	16.55	14.50	14.50	12.99	15.16	-	6.57	7.35
16 *Cuora trifasciata*	14.29	13.67	15.88	13.56	13.56	15.54	17.35	13.10	13.10	16.33	15.54	15.54	12.48	13.81	9.26	-	6.63
17 *Cuora mouhotii*	14.33	13.85	16.64	13.90	13.90	16.31	16.55	13.42	13.42	16.55	16.31	16.31	13.51	13.85	11.02	9.72	-

poorly supported *M. mutica*, *M. annamensis*, "*M. iversoni*", *M. leprosa*, and *M. caspica* assemblage (DI = 2; PP = 61%). Within this large group, *M. mutica*, *M. annamensis* and "*M. iversoni*" form a strongly supported clade (BP = 99; DI = 15; PP = 100%). In fact, inclusion of both *M. annamensis* and "*M. iversoni*" render *M. mutica* paraphyletic; two *M. mutica* (ROM 25613, 25614) are more closely related to *M. annamensis* and "*M. iversoni*" than they are to a Chinese *M. mutica* (MVZ 230476) (BP = 100%; DI = 36; PP = 100%). Within this "*mutica* complex", *M. annamensis* and "*M. iversoni*" are weakly allied (BP = 60%; DI = 1; PP = 86). This entire "*mutica* complex" is then sister to a weakly supported *M. leprosa* and *M. caspica* clade (DI = 1). Finally, both MP and Bayesian analyses suggest that *M. rivulata* is sister to a monophyletic clade containing the rest of *Mauremys*, but this phylogenetic arrangement receives almost no statistical support (DI = 2; PP = 60%).

Discussion

Phylogenetic relationships. - Both MP and Bayesian phylogenetic methods show that *M. japonica* is a member of a clade containing *M. nigricans*, *M. reevesii*, and *M. sinensis*, exclusive of other *Mauremys*. The *M. japonica*, *M. nigricans*, *M. reevesii*, and *M. sinensis* clade is joined to a poorly supported *M. mutica*, *M. annamensis*, *M. leprosa*, and *M. caspica* assemblage. Within this grouping, *M. mutica* and *M. annamensis* form a solid clade, congruent with shell and scute data (Iverson and McCord, 1994), other molecular data (Barth et al., 2004; Spinks et al., 2004) but not 12S and 16S mtDNA data (Honda et al., 2002a). Our analyses further suggest that *M. mutica* is paraphyletic. Two *M. mutica* (ROM 25613, 25614) purchased in Vietnam are more closely related to *M. annamensis* than they are to topotypic *M. mutica* (MVZ 230476) from China. We tested the paraphyly of *M. mutica* by constraining the MP searches to recover only those trees that produce a monophyletic *M. mutica*. The shortest two trees generated by the constraint search are 697 steps long (CI = 0.594; RI = 0.636), 36 steps longer than the unconstrained MP tree. The two-tailed Wilcoxon signed-ranks test (Templeton, 1983) fails to support (P < 0.0001) the monophyly of *M. mutica*. The *mutica* complex is linked to a tenuous *M. leprosa* and *M. caspica* group. Lastly, both MP and Bayesian phylogenetic analyses tentatively place *M. rivulata* sister to a monophyletic clade containing the remaining ingroup taxa.

Genetic Variation. - Our samples of *M. leprosa* from Spain and Morocco, and *M. caspica* from Iran and Bahrain, show no intraspecific haplotype diversity

(Table 1), yet exhibit sizeable morphological variation (Busack and Ernst, 1980). This discrepancy between intraspecific mtDNA diversity and geographic variation seems to be common among turtles (e.g., Lenk et al., 1999; Starkey et al., 2003) and may be related to extensive phenotypic plasticity or the slow rate of molecular evolution in turtles (Avise et al., 1992; Lamb et al., 1994).

In contrast, most interspecific mtDNA variation appears extensive, with uncorrected sequence divergences higher than 8% between a number of ingroup taxa (Table 1). Additionally, the mitochondrial sequence divergences between *M. rivulata* and *M. caspica* (Table 1), formerly considered conspecifics (Fritz and Wischuf, 1997), are equivalent to or greater than the genetic distances observed between other congeneric emydid and batagurid turtles (e.g., Feldman and Parham, 2002; Starkey et al., 2003; Stuart and Parham, 2004). Hence, these mtDNA data, together with the differing shell morphologies, distinct color patterns, and unique habitat preferences of *M. rivulata* and *M. caspica* (Busack and Ernst, 1980), support the recent elevation of *M. rivulata* as a distinct evolutionary lineage independent of *M. caspica* (Fritz and Wischuf, 1997).

Mauremys annamensis, a robust batagurid endemic to central Vietnam, is characterized by extensive axillary buttresses, a massive bridge, a slightly tricarinate and high-domed shell, a vividly striped head and neck, and reverse sexual size-dimorphism (McDowell, 1964; Iverson and McCord, 1994). The taxon is so distinctive it was once placed into its own genus, *Annamemys* Bourret 1939. McDowell (1964) originally demonstrated that *M. annamensis* and *M. mutica* share a number of derived features and Iverson and McCord (1994) subsequently confirmed a close kinship between these taxa with shell measurements. Hence, the close relationship revealed by our mitochondrial genes is not novel. What is surprising, however, is that *M. annamensis* differs from Vietnamese *M. mutica* and our "*M. iversoni*"-like hybrid by only two transitions. Furthermore, this clade shows a roughly 6% uncorrected sequence divergence from topotypic *M. mutica* from Zoushan Island, Zheijung Province, eastern China. In contrast, distantly collected samples of *M. leprosa* and *M. caspica* show no such intraspecific mtDNA variation (Table 1). These data question our ideas of species limits within *Mauremys*. Is *M. annamensis* a distinct species? Does *M. mutica* represent multiple species?

Several potential hypotheses might account for these unexpected results. *M. annamensis* may simply represent a recent species, derived from *M. mutica*, or even a geographical variant of *M. mutica*. The dramatic morphological differences exhibited by *M. annamensis* could reflect intense selection and rapid phenotypic evolution while the minute mitochondrial divergences and paraphyly represent the nature of speciation and unsorted polymorphism. Alternatively, there may be historical or ongoing introgression between *M. annamensis* and Vietnamese *M. mutica*, perhaps facilitated by selection.

Two additional hypotheses involve the possibility of hybridization. While our specimen of *M. annamensis* conforms to the species description, it was acquired from a Chinese turtle farm (Appendix 1) where *M. annamensis* and *M. mutica* are reared together in large numbers (J.F. Parham, pers. obs.). Hence, our *M. annamensis* could be a captive hybrid between *M. annamensis* and *M. mutica*, though we find no morphological characters supporting this notion. Ideally, we would examine the morphology and compare the sequences of a wild-caught *M. annamensis* to our sample, but to our knowledge, no tissued, field-collected vouchers of *M. annamensis* exist in collections; all modern museum specimens of *M. annamensis* have been obtained from either animal markets or the pet trade.

Another possibility is that the Vietnamese *M. mutica* could be hybrid offspring of female *M. annamensis* and male *M. mutica*, accounting for the scant mtDNA differences between Vietnamese *M. mutica* and *M. annamensis* and the sizeable divergences between these samples and topotypic *M. mutica*. Although the "Vietnamese *M. mutica*" are phenotypically similar to typical *M. mutica*, their darker coloration is evocative of *M. annamensis*. Both Barth et al. (2004) and Spinks et al. (2004) found substantial mitochondrial variation between *M. mutica* and *M. annamensis*, but we do not know the provenance or morphology of their samples.

The hybridization of batagurid turtles has lead to other cases of taxonomic confusion (Parham and Shi, 2001; Parham et al., 2001; Shi and Parham, 2001; Wink et al., 2001; Spinks et al., 2004) and cannot be discounted here. Unfortunately, our small sample size prohibits us from effectively evaluating these hypotheses. Clearly a more detailed genetic study is needed to unravel this problem. With our present knowledge, any change in conservation policies for *M. annamensis*, one of the world's most poorly known turtles, would be premature.

Biogeography. - The distribution of *Mauremys* is characterized by a major break between the Zagros Mountains of western Iran (easternmost *M. caspica*) and the Annamite Mountains of central Vietnam (range of *M. annamensis*). This disjunction includes the entire Indian subcontinent (home to a diverse, endemic batagurid fauna), and the inhospitable Tibetan plateau. We suggest that the collision of India into Asia may be the vicariant event responsible for the current distribution of *Mauremys*, as proposed for anguine lizards (Macey et al., 1999). Molecular data are ambiguous on this point.

Given that neither eastern nor western species assemblages appear monophyletic (though a Wilcoxon signed ranks test topology test cannot discount this hypothesis [$P = 0.35$]), the current divergences between the living species may have occurred before the development of the Indo-Tibetan gap. The collision and subsequent uplift of the Tibetan plateau took place in multiple stages between 50 and 10 MYBP (Shackleton and Chang, 1988; Dewey et al., 1989; Windley, 1988). Hervet (2004) attributed some Paleogene (>50 MYBP) European fossils to the stem of *Mauremys*, but did not investigate their relations to east Asian *Mauremys*. In addition to employing additional molecular markers to vouchered museum specimens, the integration of all extant *Mauremys* into analyses of morphological characters and fossil taxa will be necessary to unravel the historical biogeography of this clade of turtles.

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Appendix 1.

Specimens used and GenBank Accession numbers for DNA sequence data. Acronyms are: MVZ = Museum of Vertebrate Zoology, Berkeley, California; ROM = Royal Ontario Museum, Toronto, Ontario; AF or AY = GenBank (http://www.ncbi.nlm.gov).

Mauremys annamensis - Purchased in turtle farm in Hainan Province, China, no real locality data; MVZ 238937; AY337338, AY337346. *Mauremys caspica* - Field collected on Bahrain Island, Bahrain; MVZ 230971; AY337339, AY337347. *Mauremys caspica* - Field collected in West Azarbaijan Province, Iran; MVZ 234281; AY337340, AY337348. "*Mauremys iversoni*" - Purchased in turtle farm in Hainan Province, China, no real locality data; MVZ 230475; AF348275, AF34281. *Mauremys japonica* - Pet trade specimen, no locality data; MVZ 234647; AY337341, AY337349. *Mauremys leprosa* - Field collected in Tetouan Province, Morocco; MVZ 178059; AY337342, AY337350. *Mauremys leprosa* - Field collected in Cadiz Province, Spain; MVZ 231989; AY337343, AY337351. *Mauremys mutica* - Field collected in Zoushan Island, Zhejiang Province, China; MVZ 230476; AF348262, AF348278. *Mauremys mutica* - Purchased from a turtle trader in Yen Bai Province, Vietnam; ROM 25613; AF348260, AF348279. *Mauremys mutica* - Purchased from a turtle trader in Yen Bai Province, Vietnam; ROM 25614; AF348261, AF348280. *Mauremys rivulata* - Field-collected in Bursa Province, Turkey; MVZ 230212; AY337344, AY337352. *Mauremys* (=*Ocadia*) *sinensis* - Field-collected in Hainan Province, China; MVZ 230479; AY337345, AY337353. *Mauremys nigricans* - Pet trade specimen, no locality data, MVZ 130463; AF348264, AF348289. *Mauremys reevesii* - Pet trade specimen, no locality data, MVZ 230533; AF348263, AF348288. *Cuora picturata* - Purchased from a turtle trader in Dong Nai Province, Vietnam, ROM 37067; AF348265, AF348292. *Cuora trifasciata* - Pet trade specimen, no locality, MVZ 230636; AF348270, AF348297. *Cuora mouhotii* - Purchased from a turtle trader in Bac Thai Province, ROM 35003; AF348273, AF348286.

A Preliminary Report on Southeast Asia's Oldest Cenozoic Turtle Fauna from the Late Middle Eocene Pondaung Formation, Myanmar.

J. Howard Hutchison[1], Patricia A. Holroyd[1], and Russell L. Ciochon[2]

[1]*Museum of Paleontology, 1101 Valley Life Sciences Building, University of California, Berkeley, California, 94720, U.S.A.*

[2]*Departments of Anthropology and Pediatric Dentistry, University of Iowa, Iowa City, Iowa, 52242, U.S.A.*

Abstract. - Late middle Eocene fossils from the Pondaung Formation of central Myanmar document Southeast Asia's oldest Cenozoic turtle fauna. Although the material is fragmentary, seven distinct turtle taxa are recognized. These include a podocnemid pleurodire, anosteirine and carettochelyine carettochelyids, two or more trionychine trionychids, and a testudinid. Of these, only the carettochelyine carettochelyid is complete enough to recognize as a new taxon, *Burmemys magnifica*, gen. et sp. nov. The Pondaung turtle fauna is one of the best known of its age from Southeast Asia but comparisons with the limited literature of the Eocene faunas from China, Mongolia, and the Indian subcontinent indicate it is probably biogeographically unique. Among the recognized genera, only *Anosteira* is known from other Eocene Asian localities, and the presence of pleurodires is unusual.

Key words. - Reptilia, Testudines, Carettochelyidae, *Burmemys*, Myanmar, Pondaung Formation, Paleontology, Eocene.

Introduction

The origins of Southeast Asia's herpetofauna are poorly understood, as there are few fossils that document the origin of the major groups inhabiting the region. The oldest known herpetofauna from this region is from the Pondaung Formation, a late middle Eocene (approx. 37 Ma) set of rocks exposed in the Chindwin-Irrawaddy Basin of Myanmar (formerly Burma). The Pondaung fauna is best known for its mammalian fauna (e.g., Colbert, 1938; Tsubamoto et al., 2000), and little attention has been devoted to the remainder of the fauna. In prior reports, Buffetaut (1978) noted the presence of both unidentified crocodilians and dyrosaurids; Sahni (1984) and Rage (1987) noted unidentified Lacertilia. These reports were based primarily on a rather limited collection made by Barnum Brown in 1922 and housed in the American Museum of Natural History, New York. Savage and Russell (1983) and Broin (1987) list "Pelomedusid/Emydidae", "Carettochelyoidea", and trionychids from the Pondaung. Outside the Pondaung region, the only other report of turtles from Southeast Asia is Ducrocq et al.'s (1992) mention of two types of ?Emydidae from the late Eocene site of Krabi, Thailand. Here we present a preliminary description of the turtles based on a more thorough study of these collections, and additional collections in the University of California Museum of Paleontology, Berkeley, California.

Localities and age. - Fossils occur in a number of localities occurring in the upper 100+ meters of the otherwise marine Pondaung Formation. The majority of the specimens discussed here come from localities to the west and northwest of Mogaung village, Myaing Township, central Myanmar (Fig. 1), that have been collected intermittently over the past 80 years. As a consequence, most specimens have limited, descriptive locality data that provides locations based on distances from known villages. Recent fieldwork has provided detailed, GPS based mapping of the most productive outcrops and permit us to place most of the historic localities in a more accurate and stratigraphically detailed framework. Those localities we can place with confidence are shown in Figure 1. Localities whose positions are approximate are shown with dashed lines. Concordances for localities that have been published under more than one name or number are provided in the caption of Figure 1 and are based on Colbert (1938), maps on file at the American Museum of Natural History, field notes of J. Wyatt Durham and Donald E. Savage on file at the University of California Museum of Paleontology, data contained in Tsubamoto et al. (2000, 2002) and Gunnell et al. (2002), and field observations by PAH and RLC.

Fossils occur in place and as erosional lag coming out of reddish to purplish mudstones (Fig. 2 A-C). Fossil wood is also commonly found (Fig. 2D), attesting to the presence of the ancient forest. Soe et al. (2002) interpreted sediments including these localities as swale-fills and/or paleosols deposited in an ancient floodplain; stratigraphic sections for these localities are contained in Gunnell et al. (2002). Based on comparisons of temporal distribution and faunal resemblance data of the

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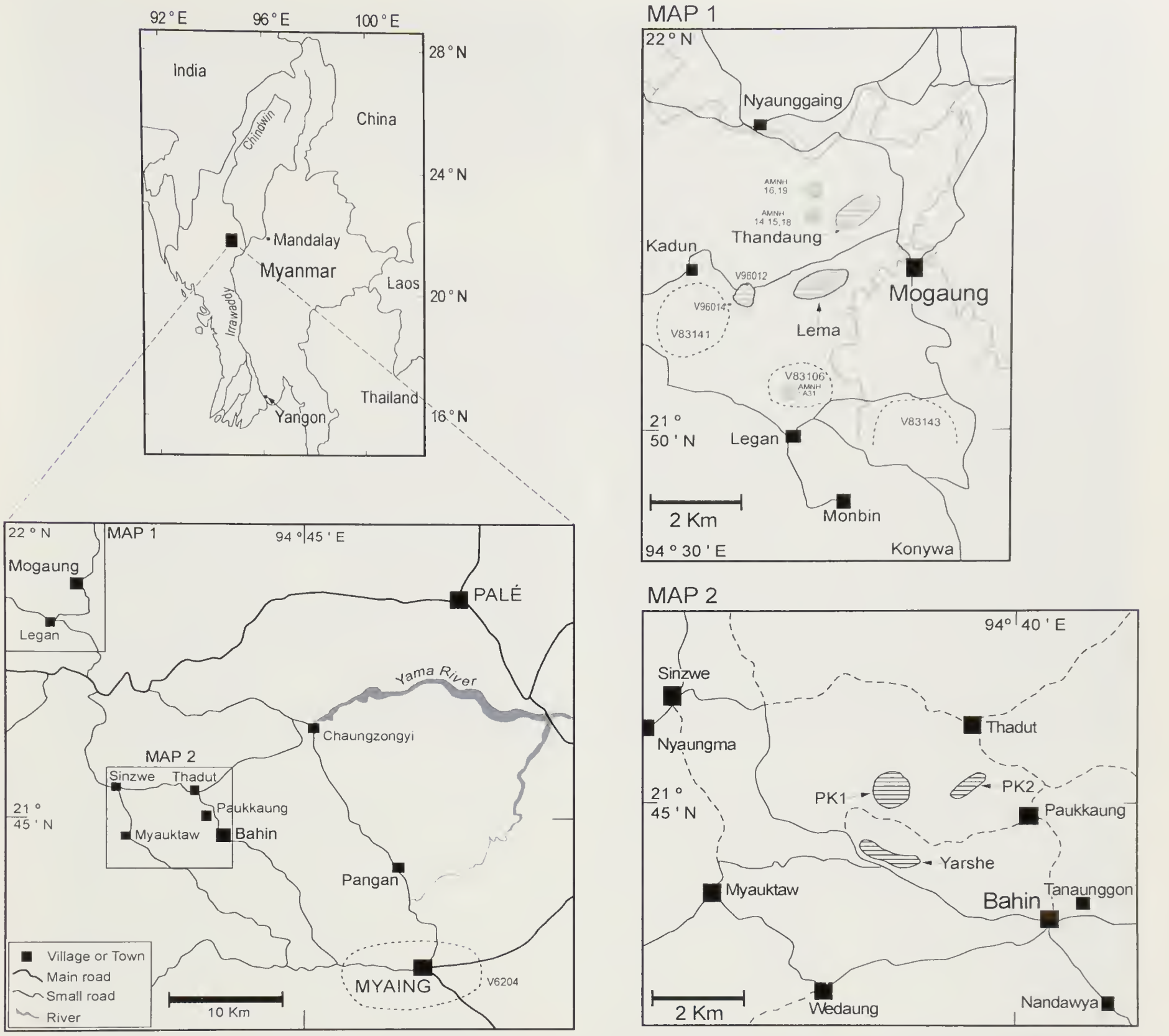

Figure 1. Locality Map of Pondaung Formation localities. V78090=Thandaung kyitchaung and possibly AMNH localities A14-16, 18-19; V83106, 3.5 mi SW of Mogaung = AMNH A31; V83111 "1.25 mi NW Paukkaung" probably equals Pk2; V83116 probably equals Yarshe kyitchaung. V96001-V96002 = AMNH A22 and Lema kyitchaung; V98019 "Thidon or near Bahin", possibly equal to Pk1 or Pk2.

Pondaung mammalian fauna with other Asian and North American mammal faunas, as well as additional constraining evidence from marine invertebrates, Holroyd and Ciochon (1994) concluded that the Pondaung fauna is best considered latest middle Eocene in age and broadly contemporaneous with Asian faunas assigned to the Sharamurunian Land Mammal Age, a finding confirmed by recent fission-track dates that provide a date of 37.2 +/- 1.2 Ma (Tsubamoto et al., 2002).

Abbreviations. - AMNH, American Museum of Natural History, New York, New York, U.S.A.; UCMP, University of California Museum of Paleontology, Berkeley, California, U.S.A.

Systematic Paleontology

Testudines Batsch, 1788
Pleurodira Cope, 1865
Pelomedusoides Cope, 1868
Podocnemididae Cope, 1868
?Podocnemididae unident.

Referred Material. - UCMP locality V83108: UCMP 153798, right peripheral 3. UCMP locality V83113: UCMP 147052, partial left hypo-xiphiplastron. UCMP locality V96002: UCMP 142245, left incomplete epiplastron.

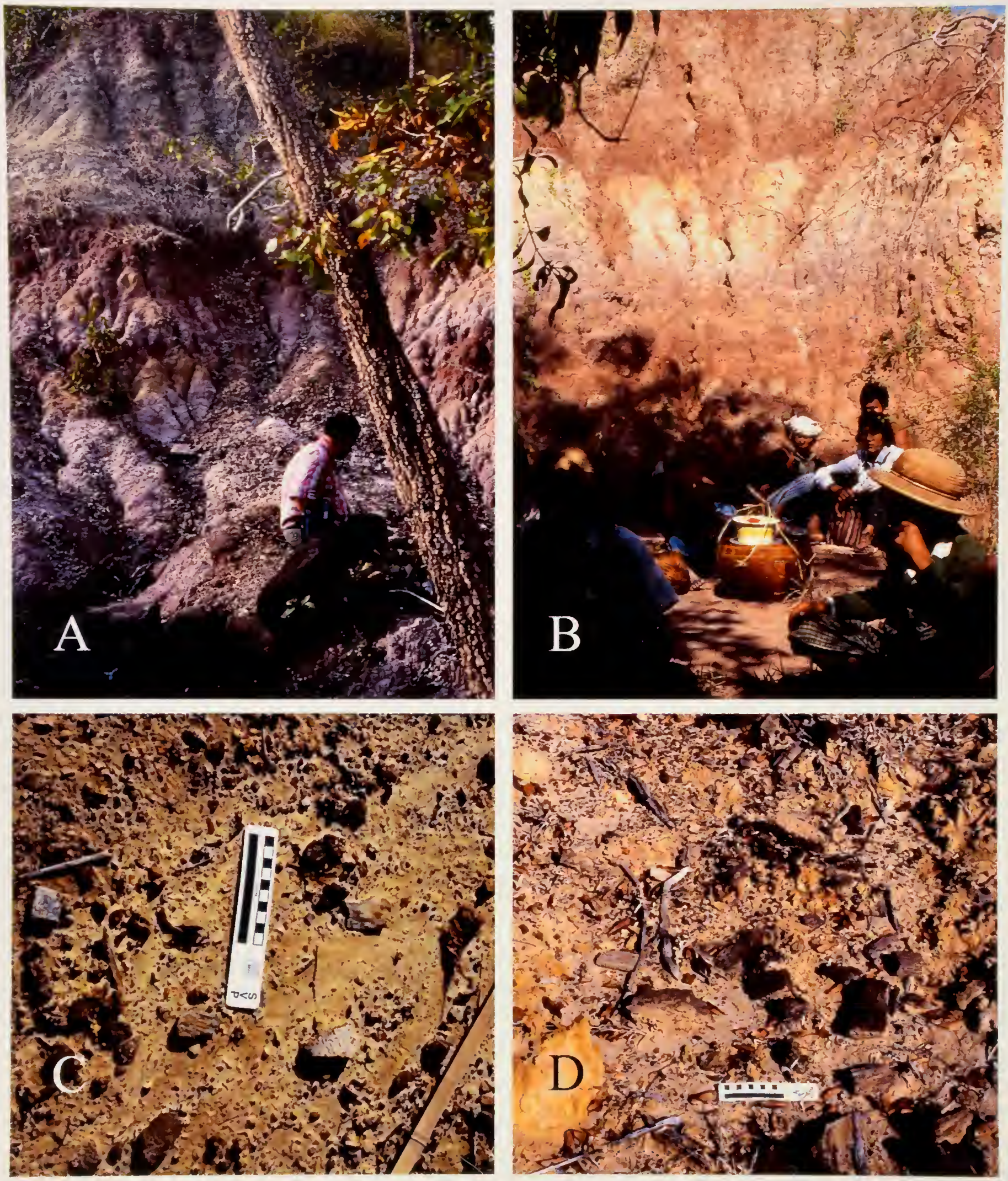

Figure 2. Fossil localities of the Pondaung Formation. **A**. UCMP locality V96001, Lema kyitchaung; **B**. UCMP locality V96002, Lema kyitchaung; **C-D**. UCMP locality V96007, near Mogaung, showing the common occurrence as float of both turtle bone (**C**) and petrified wood (**D**) on the surface.

Description. - The epiplastron (UCMP 142245, Fig. 3A) lacks the posterolateral part but is otherwise well preserved. The scale covered surfaces are very finely textured with delicate but well-defined sulci. Faint growth corrugations are present on the gular scale (extragular of Hutchison and Bramble, 1981). There is a prominent anteriorly-projecting gular spur, and the epiplastron margin is distinctly concave between the midline and the gular spur. There is an intergular scale (gular of Hutchison and Bramble, 1981) spanning the midline that projects anteriorly into the anterior embayment. The scales overlap extensively onto the dorsal surface with little exposure of the visceral surface. The intergular expands slightly posteriorly on the ventral surface and

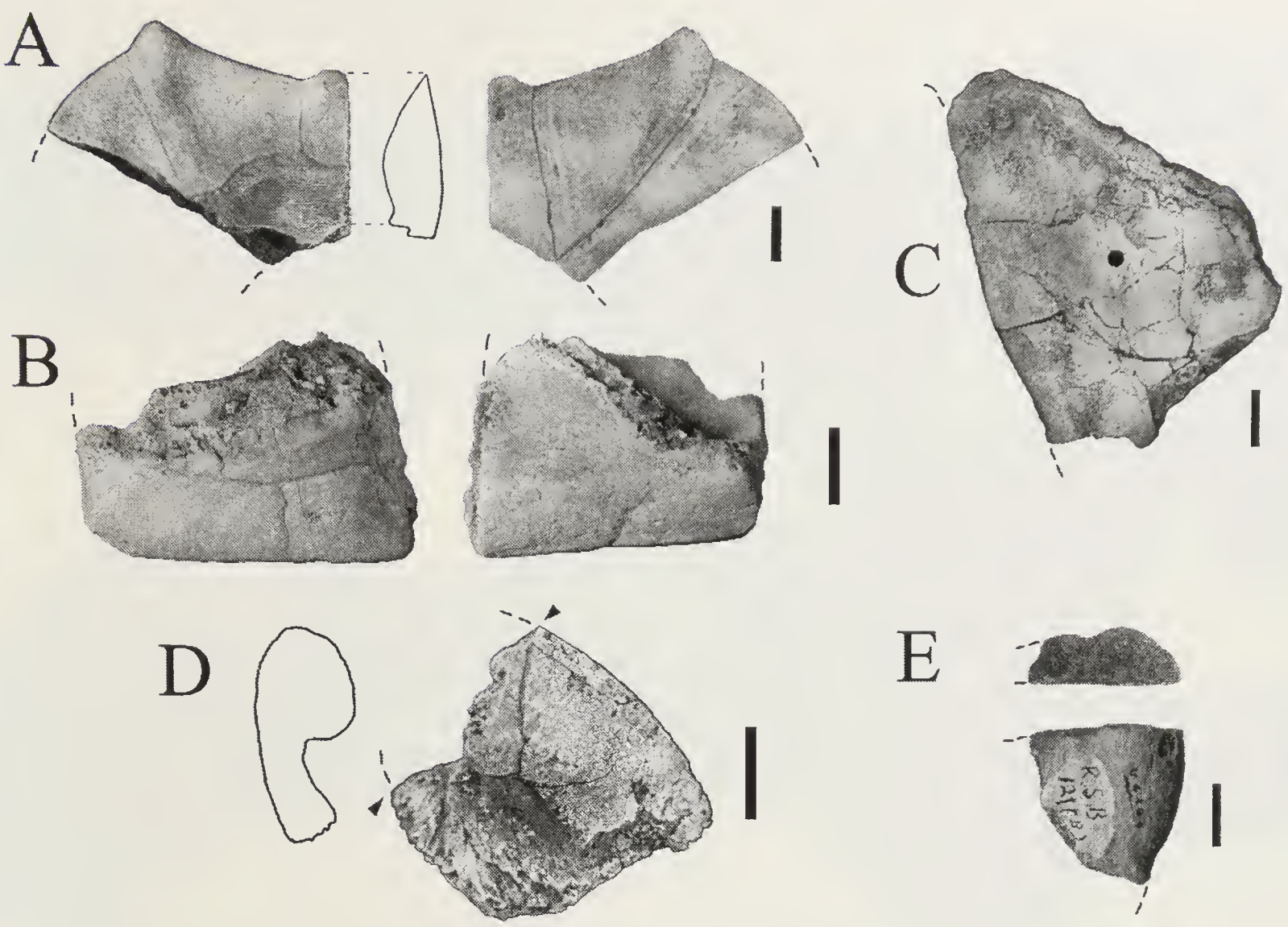

Figure 3. **A-C**. Podocnemidae? indet. **A**. UCMP 142245, incomplete left epiplastron, dorsal, medial suture and ventral views. **B**. 153798, right peripheral 3, external and visceral views. **C**.UCMP 147052, hypo-xiphiplastron fragment, dorsal view, spot indicates center of bump. **D-E**. Testudinidae. **D**. UCMP 142226, partial right epiplastron, cross-section (as indicated) and dorsal views. **E**. UCMP 149166, partial right xiphiplastron, dorsal view. Scale bars equal 1 cm.

extends onto the entoplastron. Dorsally the intergular extends slightly more than one-half the length of the inter-epiplastral suture and is parallel-sided. On the ventral surface, the gular is triangular with the lateral margins converging to a point at the entoplastron margin.

The hypo-xiphiplastron fragment, UCMP 147052 (Fig. 3C), is broken on all the edges except the free margin. It exhibits a narrow overlap of the femoral and anal scales onto the dorsal surface (less than one-fifth the transverse length as preserved). The swelling at the anterolateral corner indicates an ascendant hypoplastral buttress. The sutures are fused. A short expanse of the femoral-anal scale sulcus is preserved at the extreme posterior end. Medial to the scale margins on the dorsal side is a large elliptical swelling that has a smooth surface and may have been divided by the hypo-xiphiplastron suture.

The peripheral 3 (UCMP 153798, Fig. 3B) lacks the dorsal margin. The body of the peripheral is robust and without a change in plane between the pleural and marginal surfaces. The surface is smooth and unsculptured. The sulci are shallow but well defined. The free margin is acutely angled. On the visceral side, the marginal scales rise up from only about one-third of the peripheral depth. There is no indication of an axillary scale. The finely dentate suture for the hyoplastron buttress rises anteriorly and may have overlapped peripheral 2-3 suture. There is a gap in the hyoplastral suture near the posterior margin, for passage of the musk duct. The length between the anterior and posterior sutures along the free margin of the peripheral is 37.9 mm.

Discussion. - The dorsal scale overlap, truncated anterior margin, undivided intergular, and relatively thick epiplastra resemble selected extant or fossil Pelomedusoides (Bothremydiae, Podocnemididae, and Pelomedusidae). The prominent epiplastral spurs resemble those of the pelomedusid *Kenyemys* Wood, 1983, from the Pliocene of Kenya. However, the Pondaung form differs in the greater excavation of the gular embayment, intergular extending onto the entoplastron, and restriction of the gular scales to the epiplastra (i.e., not reaching the midline). The scale arrangement is similar to that of the podocnemidid *Neochelys* Bergounioux, 1954 (Broin, 1977; Jimènez et al., 1994) from the Eocene of Europe. *Neochelys* may also possess a relatively prominent gular spur (Broin, 1977, fig. 59), but differs in the less extensive dorsal overlap of the scales and lesser development of an epiplastral embayment.

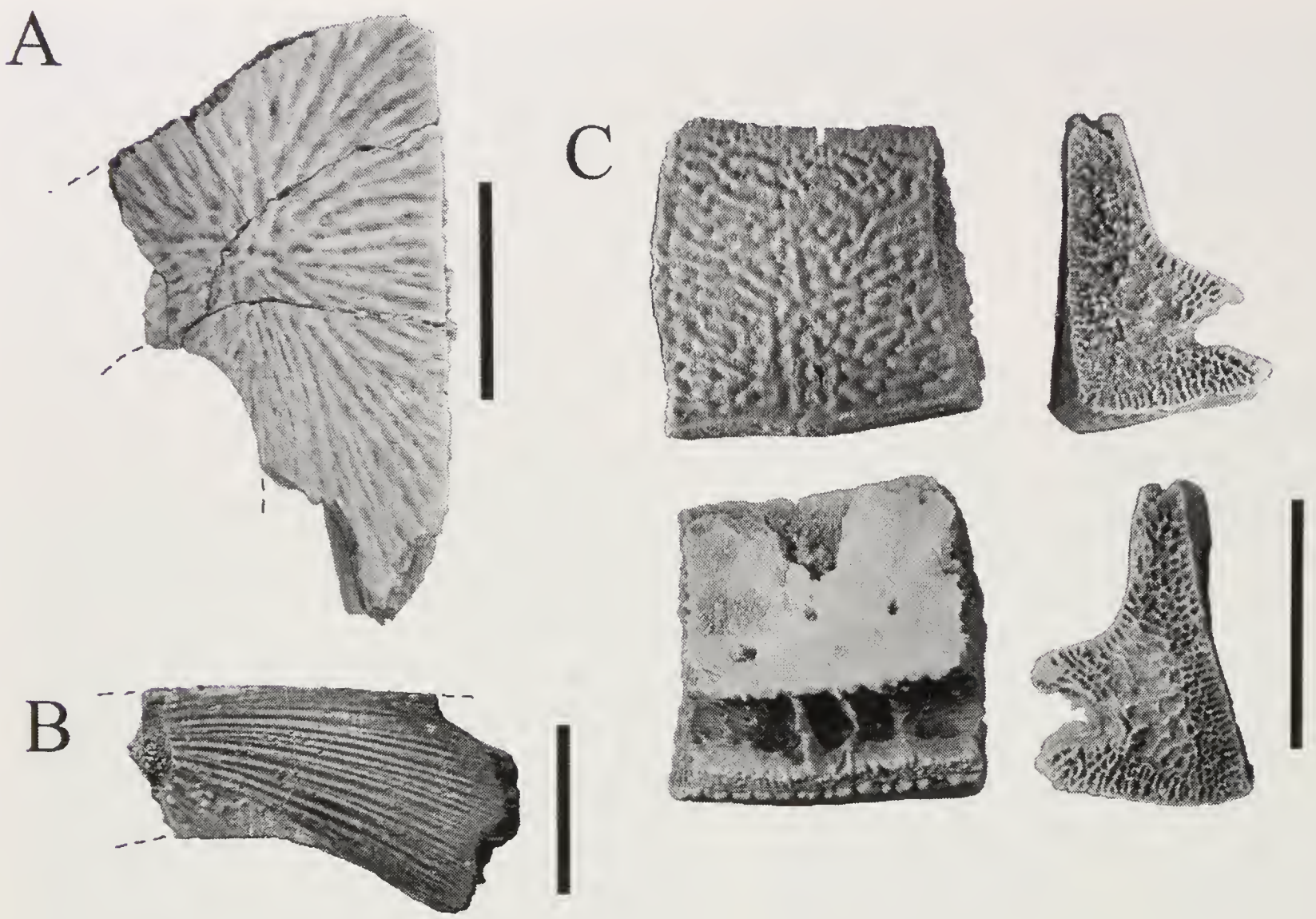

Figure 4. *Anosteira* sp., **A**. UCMP 131736, right hypoplastron, ventral view. **B**. UCMP 131737, lateral fragment of left hypoplastron, ventral view. **C**. UCMP 147030, left peripheral 6, external, posterior, visceral, and anterior views. Scale bars equals 1 cm.

The presence of a prominent musk duct on the peripheral 3, absence of an axillary scale, and strong indication of a hyoplastral buttress rising onto the first costal is consistent with *Neochelys*-like pleurodires. The hypoplastron fragment may be referable to the same taxon, but the area of the pelvic sutures is broken off.

The general similarity to at least some *Neochelys* favors a placement of the Pondaung Formation specimens in the Podocnemididae.

Cryptodira Cope, 1868
Testudinidae Gray, 1825
Testudinidae undet.

Referred Material. - UCMP locality V6204: UCMP 149166, right xiphiplastron fragment. UCMP locality V96009: UCMP 142226, partial right epiplatron.

Description. - The epiplastron (UCMP 142226, Fig. 3D) lacks the gular region. The remaining part of the free margin is greatly thickened along the anterior edge of the dorsal scale covered portion. The posterior rim of this thickened gular area overhangs the visceral surface. The ventral surface is longitudinally convex. The sutures are moderately thick and dentate.

The anterolateral part of a right xiphiplastron (UCMP 149166, Fig. 3E) is referred to the Testudinidae on the basis of the strong overlap of the femoral scale dorsally, its inflated appearance, and fairly porous surface texture.

Discussion. - The morphology of the epiplastron is typical of testudinids and a few batagurids. The rather porous bone, inflation of the gular area, and general nature of the sutures and surface texture agrees best with that of a testudinid. The overhang of the posterior gular rim is derived in testudinids and absent or poorly developed in such tortoises as *Hadrianus* Cope, 1872, *Stylemys* Leidy, 1851, *Sharemys* Gilmore, 1931, *Kansuchely*s Yeh, 1963, and *Ergilemys* Ckhikvadze, 1972. The epiplastron thus resembles more derived tortoises such as *Testudo* Linnaeus, 1858.

Testudinoidea Fitzinger, 1826, indet.

Referred material. - UCMP locality V96019: UCMP 147051, posterior part of left hypoplastron. UCMP locality V78090: UCMP 170495, partial neural. UCMP locality V98109: UCMP 170522, shell fragments.

Description. - The hypoplastron is represented by a fragment (UCMP 147052) that preserves the portion

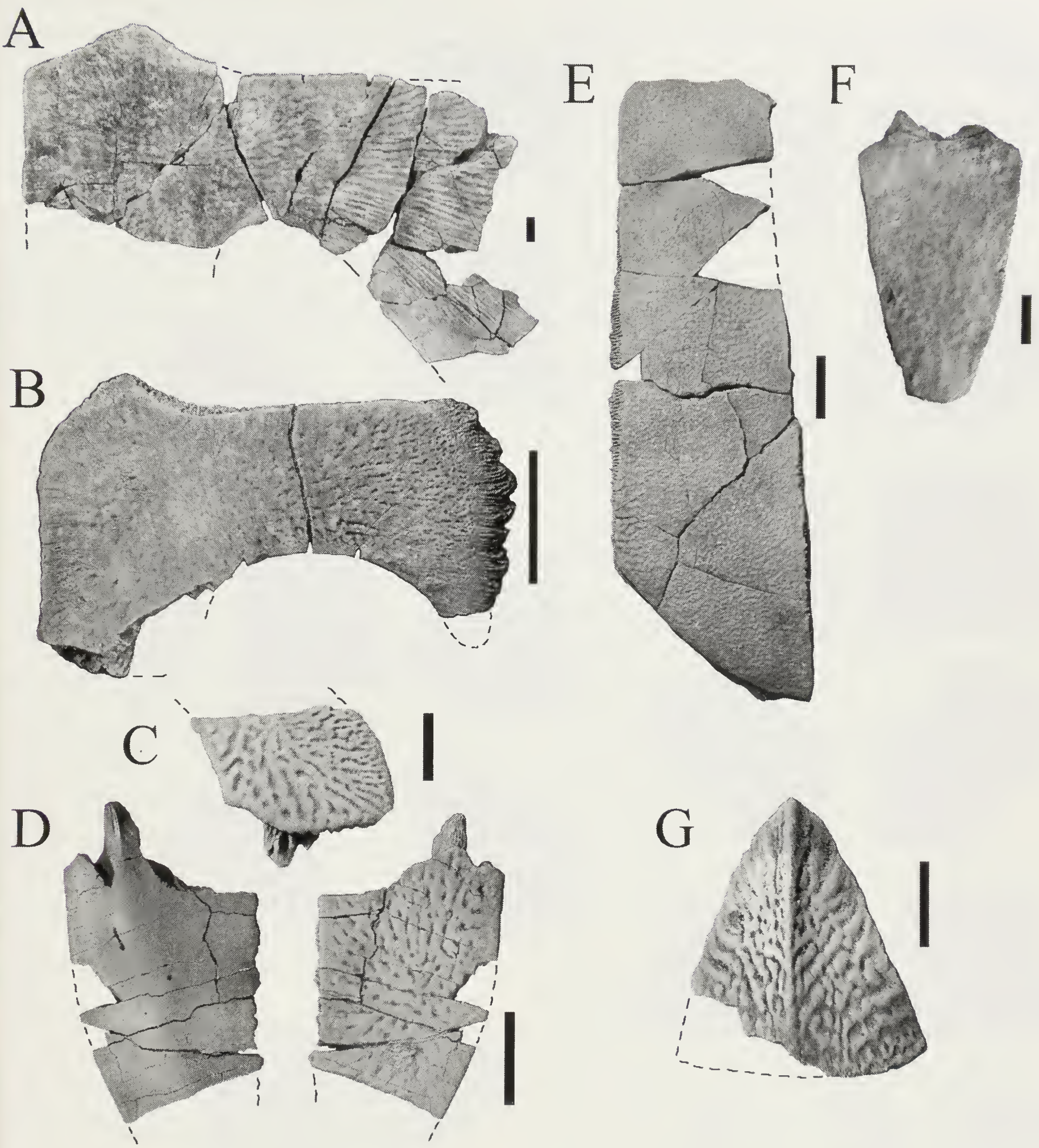

Figure 5. *Burmemys magnifica* gen. et sp. n. **A**. UCMP 61212, adult left hypoplastron (type), ventral view. **B**. UCMP 131745. juvenile left hypoplastron, ventral view. **C**. UCMP 154993, posterior part of juvenile left epiplastron, ventral view. **D**. UCMP 131747, anterior part of juvenile left xiphiplastron, dorsal and ventral view. **E**. UCMP 157444, juvenile left costal 2, external view. **F**. UCMP 147022, neural, external view. **G**. UCMP 157442, suprapygal, external view. Scale bars equals 1 cm.

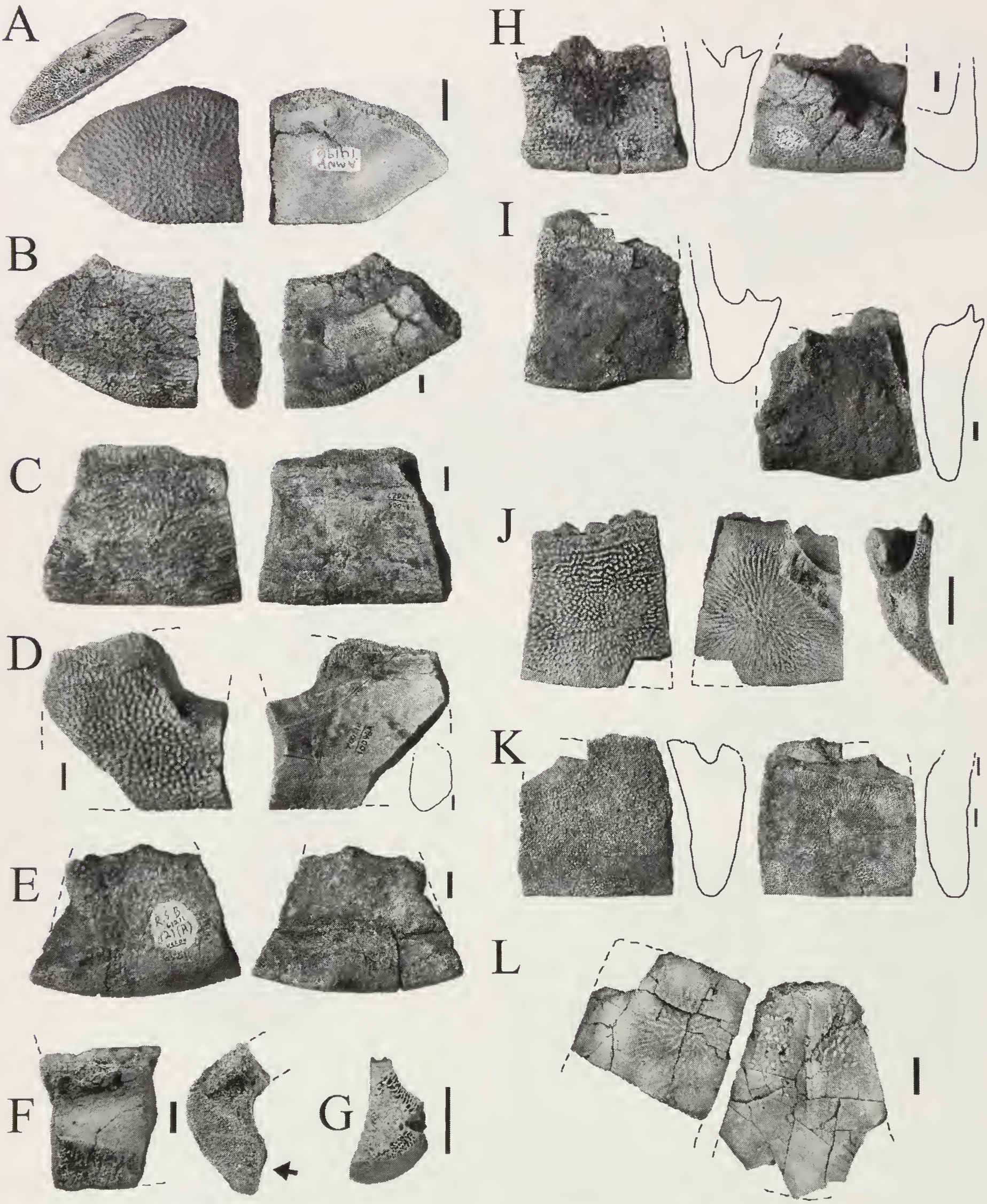

Figure 6. *Burmemys magnifica* gen. et sp. n. **A**. AMNH 14196, left peripheral 1, anterior suture, external and visceral views. **B**. UCMP 147021, left peripheral 1, external, posterior suture and visceral views. **C**. UCMP 147027, left peripheral 2, external and visceral views. **D**. UCMP 147002, left peripheral 3, external, visceral and posterior suture views. **E**. UCMP 61211, left peripheral 4, external and visceral views. **F**. UCMP 147001, left peripheral 4 fragment, visceral and posterior suture views (arrow points to flat hyoplastral suture). **G**. UCMP 131756, juvenile left peripheral 5, suture view. **H**. UCMP 61218, left peripheral 6, external, posterior suture, visceral and anterior suture views. **I**. UCMP 142223, right peripheral 7, external, anterior suture, visceral, posterior suture views. **J**. UCMP 157445, juvenile left peripheral 7, external, visceral, and anterior suture views. **K**. UCMP 142244, right peripheral 8, external, anterior suture, visceral and posterior views. **L**. AMNH 1911, left peripheral 10 and pygal, external view. Scale bars equal 1 cm.

posterior to the buttress. The free margin is slightly convex. The femoral scale distinctly but narrowly overlaps the dorsal side. The margin dorsal margin of the scale is marked by a shallow sulcus and the bone continues to thicken medially before thing nearer the midline. A partial neural (UCMP 170495) has a distinct carina with a rounded top.

Discussion. - The referred fragmentary specimens do not appear to belong to other known taxa in the fauna and agree in general morphology with testudinoids, probably testudinids or batagurids. The neural resembles those of carinate batagurids.

Carettochelyidae Boulenger, 1887
Anosteirinae Lydekker, 1889
Anosteira Leidy, 1871
Anosteira sp.

Referred material. - UCMP locality UCMP V78090: UCMP 131752, peripheral 9 or 10; UCMP 131754, hypoplastron fragment; UCMP 131755, posterior fragment of nuchal; UCMP 147115, neural. UCMP locality V83106: UCMP 131736, medial right hypoplastron fragment; UCMP 131737, lateral hypoplastron fragment; UCMP 131741, peripheral 7; UCMP 131742, peripheral 8; UCMP 131744, costal fragments; UCMP 131746, anterior fragment of a right peripheral 6. UCMP locality V96001: UCMP 147005, hypoplastron fragment; UCMP 147011, left peripheral 7. UCMP locality V96002: UCMP 147030, left peripheral 6. UCMP locality V96008: UCMP 147024, right peripheral 2. UCMP locality V96009: UCMP 142225, peripheral 9 or 10.
Description: The hyoplastron resembles those seen in typical *Anosteira* and *Pseudanosteira* Clark, 1932, and lacks the truncated anteromedial articulation of the new genus described below. This specimen differs from *Allaeochelys* Noulet, 1867, in having a narrower posterior lobe and narrower bridge area.

The peripherals are referred to *Anosteira* on the basis of their small size and well-formed sutures. Most also show the presence of weekly-defined sulci on the external surface. All the peripherals have sharp marginal carina, and the surface is finely pustulate. The gomphotic pits for reception of the plastron on peripheral 6 (UCMP 147030, Fig. 4C) lie within a longitudinal trough that traverses the peripheral. The latter is 12.6 mm along the free margin carina and 12.5 mm from the carina to the costal suture. A partial peripheral 6 (UCMP 131746) has the trough on the plastral suture filled with 8-9 vertically elongated pits and a sharp lateral carina. The two gomphotic pits on peripheral 7 also occur within a trough, but on peripheral 7 the trough is only approximately two-thirds the length of the bone. The peripheral 7 (UCMP 147011) is 12.0 mm along the carina. The specimen tentatively identified as peripheral 9 or 10 (UCMP 131752) is deeper than long (16 mm along the margin, 18 mm in depth).

The posterior nuchal fragment has the typical carettochelyid nuchal pedicle. A faint transverse sulcus is present, and another faint longitudinal sulcus near the midline is visible.

A small neural (UCMP 147115) is also referred to *Anosteira* on the basis of the small size and patterned surface, narrow length to width ratio, and low and broad central carina.

Discussion. - *Anosteira* is known from both Asia (5 species) and North America (1 species) in the Eocene. The closely related genus *Pseudanosteira* is limited to North America and distinguishable from *Anosteira* only by details of the top of the carapace. No elements in the Pondaung collection resemble *Pseudanosteira.* The presence of sulci on the peripherals, nuchal, and costal fragments indicates it should be assigned to *Anosteira.* The Pondaung specimen is most parsimoniously referred to *Anosteira* in the absence of any evidence that *Pseudanosteira* occurs anywhere in Asia. Previous records of *Anosteira* are confined to China and Mongolia.

Carettochelyinae Boulenger, 1887

Burmemys magnifica gen. et sp. nov.

Holotype. - UCMP 61212, adult left hypoplastron (Fig. 5A) from UCMP Locality V6204 (near Myaing), found by J. Wyatt Durham, late Professor of Paleontology at the University of California, Berkeley.

Paratypes. - AMNH locality "1 mile northeast of Gyat, Magwe Province": AMNH 1911, pygal, peripheral 10 fragment, and costal fragment. AMNH locality "1 mile north of Koniwa": AMNH 1919, left first peripheral; AMNH 1928, distal half of right first peripheral; AMNH 14196, partial left peripheral 1; AMNH 14197, plastron fragment. UCMP locality V6204: UCMP 61211, left peripheral 4; UCMP 61218, left peripheral 6. UCMP locality V78090: UCMP 131750, juvenile lateral hypoplastron fragment, UCMP 131751, juvenile peripheral fragment; UCMP 131753 juvenile xiphiplastron fragment; UCMP 154994, proximal costal fragment. UCMP locality V83106: UCMP 131738, juvenile right hypoplastron; UCMP 131739, juvenile hypoplastron fragment; UCMP 131745, juvenile left hypoplastron. UCMP locality V83111: UCMP 128406, right peripheral 2. UCMP locality V83116: UCMP 131748, hypoplastron fragment. UCMP locality V83143: UCMP 131747,

anterior part of left xiphiplastron. UCMP locality V96001: UCMP 147001, left peripheral 4 fragment; UCMP 147002, partial left peripheral 3; UCMP 147003, anterior peripheral fragment; UCMP 147009, neural; UCMP 147010, peripheral fragment; UCMP 147012, juvenile medial hypoplastron fragment. UCMP locality V96002: UCMP 142244, right peripheral 8; UCMP 154984, anterior peripheral fragment. UCMP locality V96008: UCMP 147021, left first peripheral; UCMP 147023, posterior peripheral fragment; UCMP 147027, left peripheral 2; UCMP 147028, partial right peripheral 1; UCMP 147029 distal fragment of a costal. UCMP locality V96009: UCMP 142223, right peripheral 7. UCMP locality V99498: UCMP 157443, neural; UCMP 157446, shell fragments.

Referred material. - UCMP locality V96001: UCMP 147004, plastron fragment. UCMP locality V83106: UCMP 131740, hyoplastron fragment. UCMP locality V78090: UCMP 131756, juvenile left peripheral 5; UCMP 154993, posterior fragment of left epiplastron. UCMP locality V99498: UCMP 157442, suprapygal; UCMP 157444, left costal 2; UCMP 157445, left peripheral 7.

Diagnosis. - *Burmemys* is distinguished from other carettochelyines by the combination of asymmetrical articulation of the hyo-hypoplastra, narrow hypoplastral bridge, and large size (estimated carapace length greater than 1000 mm).

Description. - The holotype hypoplastron (UCMP 61212, Fig. 5A) is massive. The anterior suture of the left hypoplastron consists of two sutures. The suture with the left hyoplastron is sinusoidal, curving anteromedially, and joins a distinct, straight and anteromedially-facing suture, presumably for articulation with the right hyoplastron. The ventral sculpture consists of a pattern of irregular, closely-spaced tubercles that radiate from a focal point lateral to the middle of the medial moiety. Laterally, the tubercles coalesce into ridges radiating laterally. The sutures are finely dentate and thick (13 mm). The lateral margin and posterior half of the medial part is broken away in the type, but these are preserved in the juvenile specimen (UCMP 131745, Fig. 5B). The width of the medial part of the hypoplastron measured from the apex of the inguinal notch to the plastral midline is only one-half or less of the maximum hypoplastral width. The inguinal notch is open and not confined as in *Carettochelys* Ramsey, 1887. The anterior-posterior width of the bridge area is one-half or less the width of the xiphiplastral lobe of the hypoplastron. The referred juvenile specimens exhibit the same sutural shapes as the adult (type) but the inguinal notches are shallower, sculpture less organized, and lateral extent of the lateral arm of the bridges are shorter.

The posterior part of a juvenile epiplastron (UCMP 154993, Fig. 5C) is referred to *Burmemys* on the basis of the convex curvature of the lateral margin that indicates a short and rounded anterior lobe, and an obtuse angle between the entoplastral and hyoplastral sutures indicating a short and broad entoplastron.

Two xiphiplastra (UCMP 131747, Fig. 5D; UCMP 131753) are referred to *Burmemys* on the basis of relatively larger size, converging (non-parallel) medial and lateral margins of the anterior moiety, and thinning rather than thickening toward the midline suture. Both specimens are small (proximal width of UCMP 131747 is 20 mm) and thus considered as juveniles.

The juvenile left costal (UCMP 157444, Fig. 5E) is nearly uniformly thin, parallel sided, and sculptured with a subdued and random pattern of low pustules and short ridges. The distal margin forms about a 45 degree angle to the sides. There are no sulci. The parallel sides and high angle of the distal margin indicate a second costal.

The distal end of an adult costal (UCMP 147029) is subtlety sculptured with longitudinal irregular ridges. The distal suture is weakly dentate but patent except above the rib. The rib ends protrudes prominently. Although damaged, the distal width is about 70 mm.

A large neural (UCMP 147009, Figs. 5F) is relatively narrow, lacks a midline carina, and has subtle sculpture of very shallow dimples. It has a midline length of 51 mm, maximum width of 32 mm, and maximum thickness of the lateral side of 15.4 mm.

The suprapygal (UCMP 157442, Fig. 5G) is triangular with a distinct medial carina. The surface sculpture consists of irregular vermiform ridges that radiate from the central area of the posterior margin. It is longer than wide (32.2 mm long, 31.5 mm wide).

At least nine peripheral positions are represented. The sculpture is variable consisting of distinct tubercles at one extreme to anastomosing pits and ridges at the other. The free margins of adult specimens are rounded but may be acute in juveniles. There are no indications of scale sulci.

The first peripheral exhibits distinct sutures with the first costal, nuchal and second peripheral. The free margin perimeter is asymmetrically curved. The largest specimens (AMNH 1919, Fig. 6A; UCMP 147021, Fig. 6B) have perimeter lengths of 114 and 119 mm, maximum depths of 90 and 81 mm, maximum thicknesses at the posterior suture of 33 and 27 mm, and maximum thicknesses at anterior suture of 28 and 25 mm respectively.

The two second peripherals differ in size. UCMP 147026 (Fig. 6C) is massive with a free margin length of 82 mm, maximum depth of 67 mm, and maximum thickness of the anterior suture of 20 mm. Comparable measurements of UCMP 128406 are 45, 40, and 11 mm respectively. The second peripheral is roughly rectangular in external view.

The only specimen referred to the third peripheral (UCMP 147002, Fig. 6D) is lacking the anteroventral and posterodorsal corners. The anterior part of the dorsal suture is a semi-scarf joint – probably for the rib end of the first costal. The peripheral thickens noticeably towards the posterior suture and reaches a thickness of 32 mm at the suture.

The fourth peripheral (UCMP 61211, Fig. 6E) is damaged anteriorly and dorsally and locally abraded. Its length along the lateral carina is 75 mm. The free margin curves posteromedially on the posterior moiety to form a plastral articulation. The plastral articular surface is relatively flat but deep (up to 16 mm) and without pits for the hyoplastral buttress or normal dentations, thus indicating a weakly ligamental and kinetic joint. The lateral carina is broadly rounded. The peripheral 4 fragment (UCMP 147001, Fig. 6F) also shows this rather flat and deep (19 mm) hyoplastral suture.

A small peripheral, probably a left peripheral 5 (UCMP 131756, Fig. 6G) is considered a juvenile of this species. The plastral arm is very short with a longitudinal trough enclosing a series of gomphotic pits. The lateral carina is slightly rounded and broadly upturned. The length of the lateral carina is 22 mm and has a posterior thickness of about 9 mm.

A relatively complete left peripheral 6 (UCMP 61218, Fig. 6H) has a damaged plastral margin and lacks the dorsal suture. The plastral and costal arms converge posteriorly. The plastral articulation is broken anteriorly but posteriorly has a longitudinal trough indicating interdigitation with the hypoplastron. The lateral carina is rounded and slightly upturned. The length along the lateral carina is 82 mm.

A peripheral 7 (UCMP 142223, Fig. 6I) of an adult measures 99 mm along the marginal carina, 100 mm from the carina to costal margin, posterior thickness of 29 mm and an anterior thickness of more than 45 mm. The hypoplastral suture is damaged but trough-like, extends about half-way along the medial side, and appears to have housed one or two recessed pits. The isolated peripheral 7 (UCMP 157445, Fig. 6J), a presumed juvenile, closely resembles *Carettochelys* with the hypoplastral buttress rising up the central part of the medial side. The free margin is sharp and broadly upturned. The length of the free margin is about 34 mm.

The adult peripheral 8 (UCMP 142244, Fig. 6K) is massive and slightly shorter than deep (97 mm along the lateral carina and 105 mm from the carina to costal suture). An anteriorly-deepening trough divides the medial surface into dorsal and ventral arms anteriorly.

The pygal (AMNH 1911, Fig. 6L) is distinctly trapezoidal with a short anterior side and a low but sharp medial crest. The sculpture consists of widely spaced irregular tubercles that fade out near the medial crest and free margin. An associated posterior peripheral 10 fragment has a sculpture of irregular ridges and tubercles that radial from a central focus.

Discussion. - The absence of scales and large size place *Burmemys* in the Carettochelyinae. Of the three Eocene genera of Carettochelyinae, *Burmemys* differs from all in the presence of two distinct anterior articular sutures on one of the hypoplastra. This most likely represents an asymmetrical articulation with the hyoplastra, with one of the hyoplastra extending well across the midline to form an angled articulation with the opposite hypoplastron. Even where the hyo-and hypoplastra are not mirror images with one of the hypoplastra contacting the opposite hyoplastron (e.g., *Anosteira* in Hay, 1908, Fig. 353), the midline suture remains straight as in other Paleogene carettochelyids and the plastral midline suture usually exhibits some limited kinesis. This asymmetry is not unusual in turtles, but within carettochelyids was known only to a lesser degree in some *Carettochelys*. The hypoplastron in extant *Carettochelys insculpta* Ramsey, 1887 may cross the midline to form a short angled suture with the opposite hyoplastron (AMNH 84212, and Rooij, 1915, fig. 123a). This occurs on the left hyoplastra on both of these.

Burmemys resembles anosteirines and differs from extant *Carettochelys*, *Hemichelys* Lydekker, 1887, (pl. XII, fig. 2) from the Eocene of the Punjab, and *Chorlakkichelys* Broin, 1987 (pl. 1, fig. 2) from the Eocene of Pakistan in the relatively broad inguinal notch. *Burmemys* additionally differs from *Chorlakkichelys* and *Carettochelys* in having a distinctly narrow bridge area. The general proportions of the hypoplastron resemble those of *Allaeochelys* from the Eocene of Europe (Broin, 1977, Pl. XV1, Fig. 3). The suprapygal differs from *Allaeochelys*, *Carettochelys*, *Hemichelys* and probably *Chorlakkichelys* in being longer than wide.

Burmemys is also the largest carettochelyid described to date. Based on scaling up of the elements in comparison to other carettochelyids, we can estimate that the shell length of *Burmemys* exceeded 1000 mm. This estimate suggests that *Burmemys* is among the largest turtles known, but is smaller than estimates Head et al. (1999) provided for Eocene trionychids from Pakistan, which may have reached more than 2000 mm in length, and is smaller than the giant Bridgerian trionychid from Wyoming (Gaffney, 1979).

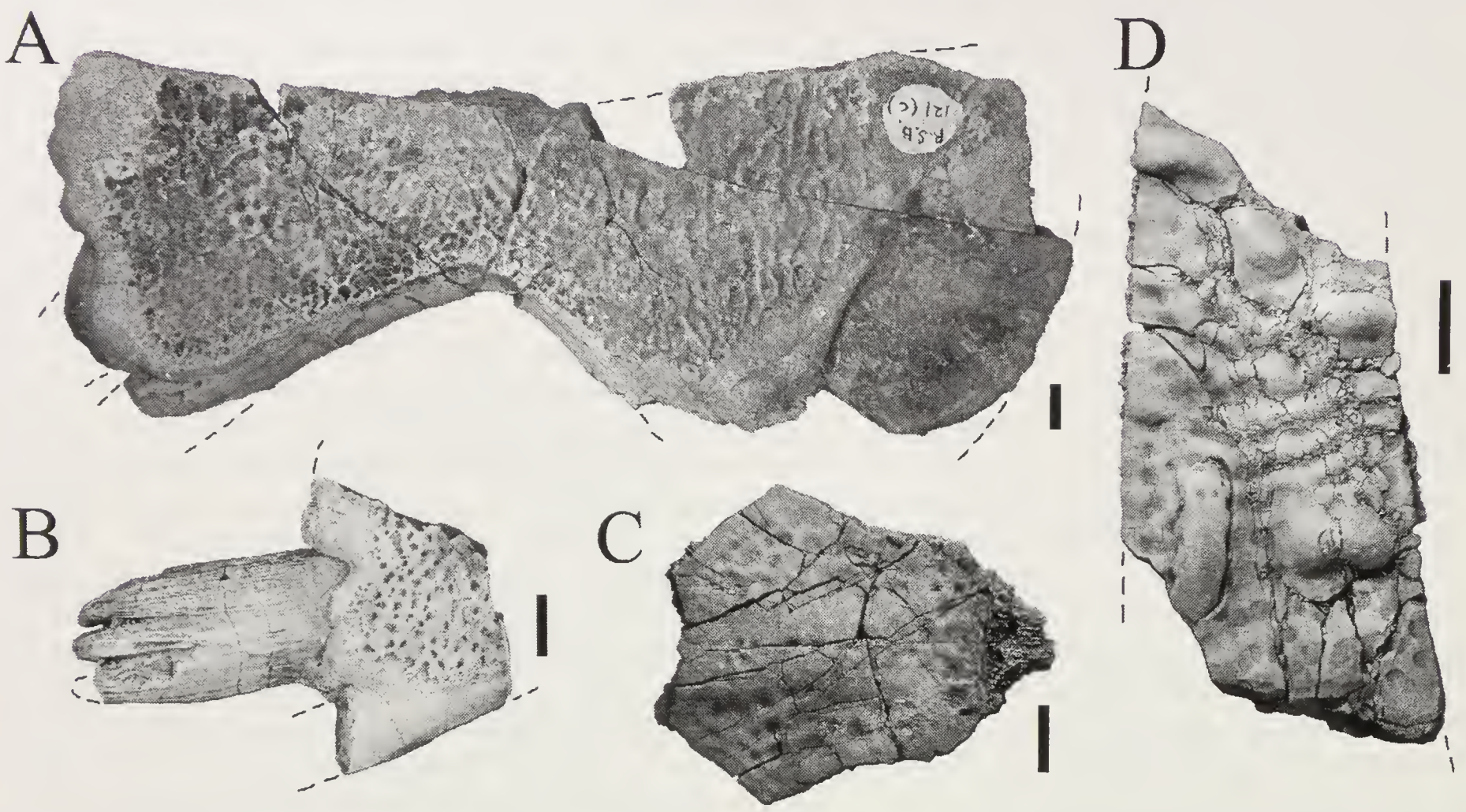

Figure 7. Trionychinae. **A**. UCMP 61213, right hypoplastron, ventral view. **B**. UCMP 1537993, fragment of right hypoplastron, ventral view. **C**. UCMP 147022, neural, external view. **D**. UCMP 170520, costal fragment, external view. Scale bars equals 1 cm.

Trionychidae Gray, 1825
Trionychinae Gray, 1825
Trionychinae genus indet.
Trionychinae, large form

Referred material. - UCMP locality V6204: UCMP 61213, right hypoplastron. UCMP locality V78090: UCMP 170497, costal fragments. UCMP locality V83116: UCMP 153799, fragment of right hypoplastron. UCMP locality V83143: UCMP 173809, plastron fragment. UCMP locality V96001: UCMP 147020, costal fragment. UCMP locality V96002: UCMP 154983, costal proximal fragment. UCMP locality V96008: UCMP 147022, neural. UCMP locality V96009: UCMP 142222, plastron fragment.

Description. - The hypoplastron (UCMP 61213, Fig. 7A) lacks the projecting spines (present in UCMP 153799, Fig. 7B) but is otherwise relatively complete. The calloused area has well defined edges and covers most of the ventral surface, except for the long offset shelf on the medial edge. The calloused area is sculptured with distinct pits and ridges, while the shelf is amorphously roughened. The buttress is composed of two protruding spikes. The posteromost of these is broken off at the base, but the larger anterior one is divided into three fluted points at its tip.

The isolated neural (UCMP 147022, Fig. 7C), probably 6 or 7, is hexagonal and narrows distinctly posteriorly. The dorsal surface is weakly sculptured, lack sulci, and is flat anteriorly but is formed into a central carina posteriorly. The neural is 46 mm long and 50 mm wide.

Discussion. - The large size of the hypoplastron and general conformation indicates a trionychine and generally resembles *Pelochelys* Gray 1864, *Chitra* Gray 1844, and *Pelodiscus* Fitzinger 1835 in these features, but differs in having a wide, unsculptured medial shelf. Additional material would be needed to refine identification.

Trionychinae, small form

Referred material. - UCMP locality V6204: UCMP 61210 plastron fragment. UCMP locality V83106: UCMP 147116, two costal fragments.

Description. - Two distal costal fragments exhibit a well-defined sculpture of pits and ridges with indications of longitudinal welts. The pattern extends to the free margin with only a slight sculpture-free zone at the free margin, suggesting an adult turtle of relatively small

size in comparison with the preceding taxon. The sculpture resembles that of a trionychine rather than a cyclanorbine such as *Lissemys* Smith, 1931.

Trionychinae, ornate form

Referred material. - UCMP locality V98109: UCMP 170520, two costal fragments.

Description. - The costal fragments (UCMP 170520, Fig. 7D) exhibit a striking sculpture of large, elongate tubercles rising above a surface composed of a generally organized pattern of longitudinal rows of shallow pits and low rides. The longitudinal axes of the raised tubercles vary from anterior-posterior to medial-lateral and are large (11-15 mm) relative to the overall size of the larger costal fragment (maximum preserved width of 32 mm). Carapace sculpturing varies between individuals and also ontogenetically, but the peculiar sculpture shows some resemblance to that seen in some extant *Aspideretes* Hay, 1904.

Discussion

In addition to the turtles, a variety of other lower vertebrates are present in the Pondaung Formation including a carcharhinid shark, *Galeocerdo* Müller and Henle 1837 (UCMP 142238), a clariid catfish (UCMP 128411), at least four species of agamid lizards (UCMP 128410, 130290, 142227, 142232), paleophid and colubroid snakes (see Head et al, in prep.), and a minimum of two crocodilians, including a pristichampsine crocodylian (UCMP 147127) and a dyrosaurid (Buffetaut, 1978).

Unfortunately, reports on Asian lower vertebrates of comparable age (Sharamurunian Asian Land Mammal Age or late middle Eocene) are few. Thus, the limited literature, combined with the fragmentary nature of the Pondaung fossils themselves, make detailed comparisons with other faunas difficult. Nonetheless, comparisons with known Sharamurunian lower vertebrate faunas reveal only a few similarities between the Pondaung and any other locality. Pleurodires are previously undescribed from Asia, although Broin (1987) notes the presence of "Pelomedusidae and/ or Emydidae" from the middle Eocene of Pakistan and Oligocene of India. An adocid was described by Gilmore (1931) from the late middle Eocene of Mongolia, but none were identified in the Pondaung assemblage. The carettochelyid genus, *Anosteira*, has been reported from age-equivalents in Manchuria (Zangerl, 1947) and Guangdong, China (Sun Ailing et al., 1992) and from slightly younger sediments in Shandong and Guangdong provinces (Yeh, 1963). The only other carettochelyines described from Asia are *Chorlakkichelys* and *Hemichelys* from the early middle Eocene of Pakistan (Lydekker, 1887; Broin, 1987), and *Burmemys* is the most easterly and southerly Eocene record of the subfamily. Trionychids, as elsewhere, are an important part of the fauna, but our material is not sufficiently diagnostic to make any meaningful biogeographic comparisons. Testudinids are widely reported in Chinese and Mongolian Eocene faunas (Gilmore, 1931; Ye, 1963), but all of these appear to be more generalized forms similar to *Hadrianus* or *Kansuchelys*. The Pondaung form appears to be more like the modern *Testudo*, and thus distinct from contemporaneous Chinese and Mongolian taxa.

Among other reptiles, the only other agamid lizard known in the Asian Sharamurunian is *Tinosaurus yuanquensis* from the Heti Formation (Li, 1991), but it is a diminutive form that bears no resemblance to the Pondaung agamids. Crocodilians are known elsewhere, but not in detail. In overall diversity, the Pondaung fauna shares more general resemblances to the better-known Irdinmanhan faunas, especially that of the Kuldana Formation of Pakistan (Broin, 1987).

Based on the fragmentary evidence available to date, several observations can be made regarding the Pondaung lower vertebrate fauna. Faunal endemicity is supported by the number of unique taxa, and the composition of the turtle fauna is unusual with trionychoids (especially carettochelyids) dominating. Faunal composition and the large size of these turtles are consistent with an interpretation of these sites as representing a warm, tropical floodplain environment, deposited fairly near shore. The aquatic habits of most of the lower vertebrates suggest that during late middle Eocene time the Pondaung region was a well-drained floodplain environment, a finding consistent with previous geological interpretations (e.g., Bender, 1983, Soe et al., 2002).

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A Review of the Comparative Morphology of Extant Testudinoid Turtles (Reptilia: Testudines)

WALTER G. JOYCE[1] AND CHRISTOPHER J. BELL[2]

[1]*Department of Geology and Geophysics, Yale University, New Haven, CT 06511*
E-mail: walter.joyce@yale.edu
[2]*Department of Geological Sciences, The University of Texas at Austin, Austin, TX 78712*
E-mail: cjbell@mail.utexas.edu

Abstract. - With an expansive geographic distribution, an excellent fossil record, and over 140 recognized extant species, testudinoid turtles constitute one of the most diverse and widespread clades of turtles. The current understanding of the distribution of morphological characters among testudinoid turtles is poor. Improved knowledge will help to facilitate accurate identification of fossil remains, and to provide a reliable morphological data set for phylogenetic analyses. We provide a critical review of skeletal and scute characters commonly utilized in previous systematic analyses of Testudinoidea. Description and illustration of character states, discussion of their distribution within Testudinoidea, and polarity determinations for 93 characters are provided. Our preliminary results indicate that ontogenetic changes in skeletal structure are an important source of variation within Testudinoidea. Sexual variation, ontogenetic variation, and intra- and inter-population variation are inadequately documented for most testudinoid taxa. Furthermore, data matrices of morphologic characters in the existing literature must be carefully reconsidered. Previously published morphologic data provide reasonably strong support for the monophyly of 'Testudinidae.' Strong morphologic support for a monophyletic 'Emydidae' is lacking, and 'batagurid' monophyly has not been rigorously tested in the literature. Because a new research cycle centered on testudinoid phylogeny is now under way, it is essential to critically re-examine the underlying assumptions and working hypotheses that have governed this field of study over the last 20 years.

Key words. - Testudines, Testudinoidea, Testudinidae, Emydidae, Bataguridae, Geoemydidae, morphology, systematics.

Introduction

Pond turtles and land tortoises (collectively, Testudinoidea) form one of the largest and most widespread clades of living turtles, with more than 140 extant species and an almost worldwide distribution. The discovery and description of many new fossil testudinoids in the last half century, combined with the emergence and ascendancy of molecular techniques in systematics, provide new opportunities to explore the evolutionary history of the group in unprecedented detail. Concomitant with the appearance of these new data sets and analytical techniques comes an increasing appreciation for conservation efforts to preserve these turtle lineages and help to secure their future in the face of increasing human predation and habitat encroachment. This is true especially for the Asian representatives of this clade (e.g., van Dijk et al., 2000) but also is relevant at a more generalized and inclusive level (e.g., Rhodin, 2000).

Our recent attempts to diagnose fossil testudinoids reliably and to place them within a phylogenetic context led to the recognition that a critical re-evaluation of morphological data and purported synapomorphies for the subclades of testudinoid turtles is desirable. A more thorough understanding of morphological data sets will provide not only a means by which molecular trees may be independently assessed, but also will form an essential foundation for diagnosing and interpreting fossil specimens. This in turn will facilitate the integration of fossil taxa into future systematic analyses, and will enhance our understanding of the paleobiogeography and divergence times of extant lineages.

The recent flurry of published works appears to represent the beginning of a new research cycle (*sensu* Kluge, 1991) in testudinoid systematics. We suggest that an important part of this cycle will be a critical re-examination of the working hypotheses that have governed testudinoid systematics since the publication of McDowell's (1964) seminal work on the group. A key component of this will be the assessment of fundamental, often unstated, assumptions that underlie current hypotheses of relationship. Our contribution to this research cycle is the first critical reappraisal of morphological characters applied to testudinoid systematics since the work of Hirayama (1985). The emerging improvement in our understanding of testudinoid relationships based on molecular sequence data will certain-

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ly result in numerous new questions (e.g., regarding paleobiogeography, the timing of sequence and evolutionary divergences, and the evolution of morphological adaptations) that will demand a clearer understanding of testudinoid morphology.

The purpose of this paper is to present a preliminary revision and discussion of the morphological characters previously utilized in investigations of testudinoid systematics. Our goal here is not to produce a phylogenetic hypothesis (indeed, we deliberately eschew such a production), but rather to evaluate the morphological data that have been, and will be, used to generate such hypotheses. To enhance our discussion and facilitate improved communication about testudinoid morphology, we provide illustrations of all characters states we discuss.

Abbreviations. - Institution and collection abbreviations: CAS, California Academy of Sciences, San Francisco, California; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; FMNH, Field Museum of Natural History, Chicago, Illinois; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; KU, The University of Kansas Natural History Museum, Lawrence, Kansas; LMNH, Louisiana Museum of Natural History, Baton Rouge, Louisiana; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; TNHC, Texas Natural History Collections, Texas Memorial Museum, Austin, Texas; TUMNH, Tulane University Museum of Natural History, New Orleans, Louisiana; YPM, Yale Peabody Museum, New Haven, Connecticut.

Abbreviations used in figures: AB, abdominal scute; af, articular facet; an, angular; bo, basioccipital; CE, cervical scute; co, costal bone; ent, entoplastron; epi, epipterygoid; fdm, foramen dentofaciale majus; fr, frontal; fpp, foramen palatinum posterius; HU, humeral scute; hyo, hyoplastron; hypo, hypoplastron; ju, jugal; MA, marginal scute; mx, maxilla; ne, neural bone; pa, parietal; pal, palatine; PEC, pectoral scute; pf, prefrontal; PL, pleural scute; pm, premaxilla; po, postorbital; pt, pterygoid; qj, quadratojugal; qu, quadrate; VE, vertebral scute; vf, vomerine foramen; vo, vomer.

Material and Methods

We examined 309 testudinoid specimens representing 93 species, but focused our efforts on 46 representative species. The list of specimens examined is provided in Appendix 1. Turtle shell nomenclature follows Zangerl (1969) and cranial nomenclature follows Gaffney (1972). Of the 46 focal species, most were recognized as valid species by Ernst and Barbour (1989), with the exception of *texana*, which they placed within '*concinna*.' Generic allocations for testudinoid species varied widely over the last 50 years and are subject to differing opinions today, particularly because the monophyly of many testudinoid genera remains untested. We consequently suppress the use of generic names wherever possible and use species epithets only. This procedure also has the advantage of precisely associating observations with species only instead of higher taxonomic categories. Most extant turtles have distinct species names, but among those turtles discussed in this review the species epithets *insculpta*, *nelsoni*, *oculifera*, *ornata*, and *platynota* each appear twice (*insculpta* under *Glyptemys* and *Carettochelys*; *nelsoni* under *Pseudemys* and *Terrapene*; *oculifera* under *Graptemys* and *Psammobates*; *ornata* under *Pseudemys* and *Terrapene*; *platynota* under *Geochelone* and *Notochelys*). For clarity in these instances, we indicate our usage with a single-letter generic abbreviation. A complete list of all currently recognized testudinoid species and all outgroup species used herein is provided in Appendix 2 together with a list of their various generic assignments used in the last 50 years.

Our use of the classic higher categories is always restricted to their phylogentic crown. 'Emydinae' (sensu McDowell, 1964) are also referred to as 'Emydidae,' 'emydids,' or North American pond turtles; 'Bataguринae' (sensu McDowell, 1964) as 'Bataguridae,' 'batagurids' or Asian pond turtles; and 'Testudinidae' (sensu McDowell, 1964) as 'testudinids' or (land) tortoises. We make no *a priori* assumptions of monophyly for any of these categories, and retain single quotations around these names throughout the text to emphasize our uncertainty.

We attempted to examine most significant morphological characters commonly utilized in systematic studies of testudinoids, but the majority of our observations concern the skeletal system and scute characters. Almost all characters were derived from the literature. Major sources for each category were: 'Bataguринae' (Hirayama, 1985; McCord et al., 1995; Yasukawa et al., 2001); 'Testudinidae' (Crumly, 1982, 1985, 1994); and 'Emydinae' (Gaffney and Meylan, 1988; Burke et al., 1996). Additional characters were also found in Mlynarski (1976), Shaffer et al. (1997), and other sources cited in the character discussions. With few exceptions, morphological features were examined on specimens themselves; evaluations based on previously published literature are indicated where applicable. Sexual dimorphism, ontogenetically influenced polymorphisms, and geographic variation in morphology are not well explored in testudinoid turtles. These areas are in need of much more research. A full exploration of

such variation is beyond the scope of this work, but we are able to make some preliminary observations regarding morphological change through ontogeny in some anatomical systems.

Polarizing characters with the help of outgroups proved to be a difficult task, mostly because all relevant extant sister taxa are highly specialized after more than 65 million years of independent evolution. Furthermore, hypotheses of the systematic relationships of the major groups of cryptodires reveal a highly unstable picture (e.g., Bickham, 1981; Gaffney, 1975, 1985; Gaffney et al., 1991; Shaffer et al., 1997) making it impossible to make any *a priori* decisions regarding the succession of outgroups. We consequently assessed polarity for most characters by examining select outgroup taxa and the ingroup taxa. Where polarity is not clear from outgroup comparison, we sometimes relied upon ingroup commonality. To allow full transparency, we discuss every polarity decision at the end of each character description.

Outgroup taxa include the cryptodires *caretta*, *odoratus*, *serpentina*, and *spinifera*, and the pleurodires *gibba*, *siebenrocki*, *subglobosa*, and *subrufa*. For a number of characters, especially of the shell, neither ingroup nor outgroup analysis of extant taxa proved useful. In these instances, polarity was based on literature descriptions of the "lindholmemydid" taxa *Gravemys*, *Lindholmemys*, and *Mongolemys*. These Cretaceous, Asian, fossil taxa are not well described in the literature, but sufficient material and description exists to use these taxa to help polarize character states (e.g., Khosatzky and Mlynarski, 1971; Sukhanov, 2000; Danilov and Sukhanov, 2001). The group may not be monophyletic, but putative members currently are hypothesized to sit along the phylogentic stem of Testudinoidea (Danilov and Sukhanov, 2001). We purposefully did not use the fossil taxon '*Echmatemys*' as an outgroup taxon (Hirayama, 1985), because its phylogenetic position outside of Testudinoidea or even 'Batagurinae' is not sufficiently demonstrated.

All figures were produced using digital photography and processed using Adobe Photoshop. Images were digitally enhanced using the burn and burnish tools and the unsharp mask filter option.

Taxonomic and Systematic Background. - Despite the increased attention directed towards testudinoids by scientists, hobbyists, and nonprofessional enthusiasts in the last thirty-five years, our collective conceptualization of the higher-level (beyond the specific and generic) systematics within this clade remained virtually unchanged since the work of McDowell (1964). The various taxonomies in current use owe their existence in large part to historical contexts that are not well appreciated by many authors. A brief summary is given here.

During the second half of the 19th century, a number of attempts were made to work out higher-level testudinoid relationships and to apply taxonomic conventions that were designed (to a greater or lesser extent) to communicate conceptualizations of these relationships. In his synopsis on the turtles of North America, Agassiz (1857) united all pond turtles into the Emydoidae and subdivided this group into a three monotypic subfamilies (Deirochelyoidae for *reticularia*, Evemydoidae for *blandingii*, Cistudinina for *T. ornata* and *carolina*) followed by the subfamilies Clemmydoidae (for *G. insculpta*, *guttata*, *marmorata*, and *muhlenbergii*) and Nectemydoidae (for those species currently placed in the genera *Pseudemys*, *Trachemys*, *Graptemys*, *Malaclemys* and *Chrysemys*). Most land tortoises were placed in Testudinidae by Theobald (1868); he also included all 'leaf turtles and tortoises' (e.g., *amboinensis*, *emys*, *dentata*, *grandis*, *tricarinata*) in Geoemydidae, and an eclectic group of aquatic turtles, including *megacephalum, serpentina*, kinosternids, and all remaining testudinoids, in Emydidae. Subsequently, all land tortoises (including *emys* and *impressa*) were united in the Testudinidae by Gray (1870). Those species currently placed in *Pseudemys* and *Trachemys* were assigned by Gray (1870) to the Pseudemydae; the Asian taxa *baska*, *borneoensis*, *thurjii*, *kachuga*, and *ocellata* were assigned to the Bataguridae, and all hinged pond turtles, 'true terrapins,' and 'snail-eating pond turtles' to the Holarctic families Cistudinidae, Emydidae, and Malaclemmydae, respectively.

Despite these early attempts, most subsequent authors (e.g., Boulenger, 1889; Siebenrock, 1909; Lindholm, 1929; Smith, 1931; Bourret, 1941) ignored (or were unaware of) these works and simply divided all testudinoid turtles into two speciose subgroups: tortoises (Testudinidae or Testudininae) and pond turtles (Emydidae or Emydinae). This situation remained static for nearly 100 years until the comprehensive and influential work of McDowell (1964). He not only divided all known pond turtles into several species complexes ('*Hardella*,' '*Batagur*,' '*Orlitia*,' '*Geoemyda*,' '*Chrysemys*,' '*Deirochelys*,' and '*Emys*' complexes), but also concluded that pond turtles can be divided clearly into two subgroups, the predominantly North American 'Emydinae' and the Asian and central American 'Batagurinae.' Furthermore, McDowell (1964) reasoned that tortoises are not the sister group of pond turtles, but rather were likely derived from a 'batagurine' ancestor. These conclusions were later corroborated by the first, and to date only, comprehensive morphological cladistic analysis of 'batagurine' systematics (Hirayama, 1985).

The influence of McDowell's (1964) work is best understood when considering its continuous impact on

subsequently proposed phylogenies. Despite differences of opinion regarding generic- and species-level systematic arrangements, virtually all major synthetic works in the last thirty years followed McDowell's (1964) subdivision of pond turtles into the 'Batagurinae' and 'Emydinae' (e.g., Mlynarski, 1976; Pritchard, 1979; Ernst and Barbour, 1989), even though 'Batagurinae' may best be regarded as a paraphyletic taxon (McDowell, 1964; Hirayama, 1985). The fundamental division proposed by McDowell is also reflected in more recent studies centered on using various molecular techniques to elucidate phylogeny, the majority of which dealt with treatments of in-group relationships *within* one or the other of McDowell's groups (Sites et al., 1984; Bickham et al., 1996; Carr and Bickham, 1986; Wu et al., 1999; McCord et al., 2000; Feldman and Parham, 2002; Honda et al., 2002; Iverson et al., 2002; Stephens and Wiens, 2003).

Admittedly, the list of autapomorphic characters compiled by Crumly (1985) for the 'Testudininae' compellingly corroborates the hypothesis of tortoise monophyly. However, most characters that currently unite 'Emydinae' or 'Batagurinae + Testudininae' seem to support these groupings weakly, because the derived states typically are not found within all species of the ingroup and commonly also are observed in species of the alleged sister group (e.g., Hirayama, 1985; Gaffney and Meylan, 1988). In addition, several of the characters that purportedly distinguish 'Batagurinae + Testudininae' from the 'Emydinae' probably should be considered primitive for the entire group (Gaffney and Meylan, 1988). Even if some characters do successfully unite a group, monophyly is not established until the involved characters are demonstrated to be derived within Testudinoidea. Furthermore, the simple demonstration of monophyly for a given group does not automatically imply that it must be the sister to the remaining taxa. For instance, 'Emydinae' may be monophyletic, but monophyly does not necessarily demand that 'Emydinae' be regarded as the sister to 'Batagurinae + Testudininae.' It is at least plausible that 'Emydinae' is situated within 'Batagurinae,' a possibility that is not adequately explored and tested in the literature.

Similarly, most of the groupings considered by Gray (1855, 1870) and Agassiz (1857) were not discussed in recent literature, even though they might be valid. For instance, given the considerable list of morphological similarities that are shared by hinged turtles of the New and Old World (e.g., development of a plastral hinge, reduction of posterior neural elements, fusion of the femoral trochanter, great reduction of the temporal arch) perhaps Gray (1870) was truly visionary in uniting these turtles as the 'Cistudinidae.' Only a global cladistic analysis with no *a priori* assumption regarding internal relationships can evaluate these alternatives and produce testable results. It is toward this end that we offer our critical reappraisal of morphological characters in testudinoids.

Results and Discussion

Cranium

(1) *Shape of the fissura ethmoidalis; 0 = narrow or closed, keyhole-shaped, Fig. 1; 1 = very wide, Fig. 2 (modified from Crumly, 1982, 13; Hirayama, 1985, 1; McCord et al., 1995, 5).*

The general configuration of the fissura in 'emydids' and 'batagurids' is keyhole-shaped (McDowell, 1964). Different proportions and widths are apparent (especially in the ventral part of the fissura), and were scored by Hirayama (1985) and Crumly (1982) as discrete character states. Our survey of many taxa reveals morphological intermediates, and the expression of various states appears to have an ontogenetic component in which younger individuals exhibit a relatively larger fissura, which corresponds to a less-ossified nasal cavity. However, a rather significant morphological gap can be observed between tortoises and pond turtles. For the purpose of this review, we lumped Hirayama's (1985) states into our state 0, and Crumly's (1982) into our state 1. The scoring presented by Hirayama (1985) and McCord et al. (1995) permitted phylogenetic resolution within 'batagurids', and that of Crumly (1982) within tortoises. Our revised scoring permits support only for the hypothesis of a monophyletic 'Testudinidae.'

Polarity: Pleurodires lack a defined fissura ethmoidalis. A keyhole-shaped fissura ethmoidalis is present in *spinifera*, *odoratus*, *caretta*, *serpentina*, and *Mongolemys*, and this condition is considered primitive for testudinoids.

(2) *Medial inflection of the inferior descending processes of the frontal; 0 = absent, or very small, Fig. 3; 1 = present, well-developed, medial contact present or almost present, Fig. 4 (modified from Hirayama, 1985, 2).*

In most turtles, a gutter (the sulcus olfactorius) is formed along the ventral surface of the frontals. This gutter transmits the olfactory nerve. The lateral rims of the sulcus sometimes form processes that descend ventromedially to surround the nerve from below (McDowell, 1964). According to Hirayama (1985) these processes are well-developed, or are in contact medially, in *ocellata* and *hamiltonii*. We confirm the presence of well-developed processes in these taxa and add *petersi*, *N. platynota*, and all sampled tortoises to the list. We recommend that this character not be subdivided into additional character states, because the descending processes of the frontals grow larger through ontogeny.

Polarity: A medial inflection is absent in all outgroups and the vast majority of the ingroup. We consider its presence to be derived.

(3) *Frontal contribution to the orbital rim; 0 = present, no prefrontal/postorbital contact on dorsal surface, Fig. 5; 1 = absent, frontal excluded from orbital rim by prefrontal/postorbital contact, Fig. 6 (modified from Crumly, 1982, 17; Hirayama, 1985, 3; Shaffer et al., 1997, 97; Yasukawa et al., 2001, 1).*

Three states for this character were scored by Hirayama (1985) and Yasukawa et al. (2001): frontal contribution always or usually present, frontal sometimes excluded from orbital rim, and frontal always excluded from orbital rim. Our sample size for many taxa does not permit a reliable assessment of intraspecific variation in this character, and thus our initial scores differed for some taxa from those of Hirayama (1985). We add *petersi* and *N. platynota* to the list of taxa in which the frontal appears always to be excluded. For those taxa that sometimes exclude the frontals, we confirm this polymorphic condition in *crassicollis*, and add *agassizii* and *annulata*. Our sample was too small to confirm the reported polymorphic condition in *amboinensis*, and *pulcherrima* by Hirayama (1985) and Yasukawa et al. (2001), but we scored these taxa as polymorphic based on their observations. We also followed Crumly (1982) by coding *pardalis* as polymorphic, even though we were not able to observe this in our sample. Our coding differs from that of Shaffer et al. (1997) for *Heosemys* and *reevesii*. In their analysis, they used *spinosa* (in which the frontal contributes to the orbital rim), but we used *grandis* (in which it does not). In both specimens of *reevesii* available to us, the frontal clearly does not participate in the orbital margin. Given the contrary statement by Shaffer et al. (1997), *reevesii* may be polymorphic for this character.

Polarity: The frontal participates in the orbital rim in pleurodires and *spinifera*, it is excluded in *odoratus* and *caretta*, and it is polymorphic in *serpentina*. No pattern is apparent within the ingroup. Given that the frontal clearly contributes to the orbital rim in *Mongolemys*, we consider its absence to be derived.

(4) *Contact between jugal and pterygoid: 0 = present, medial process of jugal well-developed and touching the pterygoid, Fig. 7; 1 = absent, medial process reduced, Fig. 8 (modified from Hirayama, 1985, 11, 12; McCord et al., 1995, 3; Burke et al., 1996, 23; Yasukawa et al., 2001, 4, 5).*

The jugal of most testudinoid turtles is expanded at its ventral end to form a medial process that contacts the pterygoid medially (McDowell, 1964). Presence or absence of the medial process, and presence or absence of a medial contact with the pterygoid were treated as two characters by Hirayama (1985) and Yasukawa et al. (2001). The scoring for the two characters appears to be redundant and we followed the recommendation of Gaffney and Meylan (1988) by combining them.

We confirm the loss of a medial contact between the jugal and the pterygoid in *galbinifrons*, *flavomarginata*, and *mouhotii* (Hirayama, 1985; Yasukawa et al., 2001), but we found this condition to be polymorphic in *spengleri* (also reported by McCord et al., 1995), and in *trijuga*. Our observations are concordant with those of Burke et al. (1996).

Polarity: A contact between the jugal and pterygoid in present in *spinifera*, *odoratus*, and *serpentina*, but is absent (although the two bones closely approach one another) in *caretta*. We conclude that the contact between the two bones is the primitive condition for testudinoids and that their separation is derived, a conclusion also reached by Hirayama (1985). Our polarity determination is opposite that used by McCord et al. (1995), who mistakenly claimed to have derived their polarity assessment from Hirayama (1985).

(5) *Contact between jugal and palatine; 0 = absent, Fig. 9; 1 = present, Fig. 10 (Gaffney and Meylan, 1988, F5.4).*

The presence of a contact between the medial process of the jugal and the palatine was used previously in support of a monophyletic Deirochelyinae (Gaffney and Meylan, 1988). We confirm the formerly observed distribution of this character within 'emydids' with the exception of *reticularia*, which does not exhibit a contact. A contact is present in numerous 'batagurids,' such as *borneoensis*, *reevesii*, *and hamiltonii*, but was absent in all examined members of 'Testudinidae.'

Polarity: A contact between the jugal and the palatine is present in *caretta*, *odoratus*, and pleurodires, but is absent in *spinifera* and *serpentina*. A contact is absent in *Mongolemys*. We consequently consider its presence to be derived.

(6) *Contact of the epipterygoid with the jugal; 0 = clearly absent, Fig. 11; 1 = present, or almost present, epipterygoid forms a long lateral process that approaches the jugal, Fig. 12 (Gaffney and Meylan, 1988, F8.1; Shaffer et al., 1997, 106).*

According to Gaffney and Meylan (1988) the epipterygoid and the medial process of the jugal approach one another or are in contact in *reticularia* and the various species they included in *Pseudemys* and *Trachemys*. They also noted a contact between these two elements in species they classified in *Graptemys*, but the condition in those taxa was interpreted to be a result of

the medial expansion of the jugal and not a lateral expansion of the epipterygoid, and consequently was regarded as non-homologous (Gaffney and Meylan, 1988). We confirm the contact or near contact of these two elements in *reticularia*, *decorata*, *scripta*, *alabamensis*, *P. nelsoni*, *rubriventris*, *texana*, *flavimaculata*, *geographica*, *kohnii*, *nigrinoda*, *G. oculifera*, *ouachitensis*, and *versa*, and also report it in *picta* and *terrapin*. Contact was clearly absent in the specimens of *barbouri*, *ernsti*, and *gibbonsi* we examined. We made no assessments of homology, but accept any contact between these two elements as the derived state (as was done by Shaffer et al., 1997). Among 'batagurids,' we also found a close approach in *reevesii*.

Polarity: A contact, or near contact, between the epipterygoid and the jugal is absent in all outgroups and the vast majority of the ingroup. We consider its presence to be derived.

(7) *Contact of the inferior process of the parietal with the medial process of the jugal; 0 = absent, Fig. 13; 1 = present, Fig. 14 (Hirayama, 1985, 13).*

Our coding differs significantly from that of Hirayama (1985). In *reevesii*, *N. platynota*, and *bealei* we found no contact between the parietal and jugal, although these were the only three taxa in which Hirayama (1985: table 2) scored it to be present. However, we found a pronounced contact between these two elements in *subtrijuga*, a species scored by Hirayama (1985: table 2) as lacking such a contact, but shown on his tree (Hirayama, 1985: fig. 2) as a unique 'batagurid' feature convergent with some 'emydids.' Among 'emydids,' a well-developed contact occurs in *barbouri* and other broad-headed species currently classified in *Graptemys*.

Polarity: There is no contact between the inferior process of the parietal and the medial process of the jugal in all outgroups and the vast majority of the ingroup. A contact is considered to be the derived condition.

(8) *Contact of the inferior process of the parietal with the maxilla; 0 = absent, Fig. 13; 1 = present, Fig. 14 (Hirayama, 1985, 14).*

Our coding differs from that of Hirayama (1985). According to his character matrix (table 2) a contact should be present between the inferior process of the parietal and the maxilla in *reevesii* and *mouhotii*, but his cladogram (fig. 2) indicated that the presence of a contact should be regarded as a uniquely derived autapomorphy of *subtrijuga*. We found no contact in *reevesii* or *mouhotii*. Of the testudinoid species we examined, *subtrijuga* is the only one that shows this feature.

Polarity: There is no contact between the inferior process of the parietal and the maxilla in all outgroups. Its presence is considered to be derived.

(9) *Extent of quadratojugal; 0 = quadratojugal well developed, firmly attached to jugal, Fig. 15; 1 = quadratojugal present, contact lost with jugal, Fig. 16; 2 = quadratojugal so heavily reduced that it appears to be absent in many skeletal specimens, Figs. 17, 18 (modified from Hirayama, 1985, 16; Shaffer et al., 1997, 47; Burke et al., 1996, 21; McCord et al., 1995, 6; Yasukawa et al., 2001, 7, 8).*

Variation in the structure of the temporal region of turtles was discussed in detail by Zdansky (1924) and comments specific to testudinoids were provided by Zangerl (1948) and McDowell (1964). We originally scored the reduction of the quadratojugal as three different characters: loss of contact with the jugal, loss of contact with the squamosal, and the apparent loss of the quadratojugal. All five logically possible combinations were observed, but in most testudinoid turtles the temporal arch is so slender that the contact between the quadratojugal and squamosal is commonly reduced to a sliver that would have to be scored as 'just barely present' or 'just barely absent.' We therefore abandoned our efforts to evaluate the contact between the quadratojugal and squamosal. Our observations generally agree with those of McDowell (1964), Hirayama (1985), Burke et al., (1996), McCord et al. (1995), and Yasukawa et al. (2001).

We purposefully avoid addressing the apparent lack of a quadratojugal in many species as an absence, because previous work by Zdansky (1924) showed that the quadratojugal of some 'batagurids' is so poorly ossified and connected to the surrounding elements that it tends to be lost in skeletal specimens (Figs. 17, 18). An example of this problem can be found among the many conflicting statements made regarding the presence of this element in *N. platynota* (e.g., Smith, 1931; Bourret, 1941; McDowell, 1964; Ernst and Barbour, 1989).

Polarity: The quadratojugal is present and firmly attached to the jugal in all outgroups, with the exception of chelids. Its reduction is considered to be derived.

(10) *Contribution of jugal to the rim of upper temporal emargination (Hirayama, 1985, 15); 0 = absent, Figs. 19, 20; 1 = present, Fig. 21.*

Participation of the jugal in the rim of the upper temporal emargination was reported previously in *hamiltonii* and *ocellata* (Hirayama, 1985). We confirm its presence in both species, but in one of the *hamiltonii* specimens we examined (MCZ 120333) the jugal forms a significant part of the rim only on one side of the skull; on the other side, which appears abnormal and likely represents a teratology, it does not. In all other species

available to us, the jugal does not participate in the rim. In *subtrijuga,* the jugal is excluded from the upper temporal emargination by narrow extensions of the postorbital and quadratojugal (Fig. 20).

Polarity: The jugal participates in the upper temporal rim of *spinifera*, but it is excluded in *odoratus*, *caretta*, *serpentina*, *Mongolemys*, and most pleurodires. We consider the participation of the jugal in the rim of the upper temporal emargination to be the derived condition within testudinoids.

(11) *Contact between the quadratojugal and the articular facet of the quadrate; 0 = absent, Fig. 22; 1 = present, quadratojugal sends a process ventrally along the rim of the cavum tympani and touches the lateral edge of the articular facet, Fig. 23 (modified from Hirayama, 1985, 17).*

The original character definition (Hirayama, 1985, character 17) is inappropriate, because the *jugal* does not contact the articular surface of the quadrate in any turtle except for *madagascariensis* and *dumerilianus* (Gaffney and Meylan, 1988). However, because Hirayama indicated in his tree that the only 'batagurid' taxon to exhibit this character is *subtrijuga*, we assume that he was referring to a contact between the *quadratojugal* and the articular facet of the quadrate, a characteristic of *subtrijuga* only among testudinoids. A contact between the two elements was reported previously for *reevesii* in the character matrix published by Hirayama (1985), but we conclude that this must be a publishing error, because it stands in conflict with his tree. In the specimens of *reevesii* available to us, there is no contact. It is possible that the scoring for *subtrijuga* and *reevesii* were flipped, at least in part, in the Hirayama (1985) matrix (in which the taxa were listed next to one another).

Polarity: A contact between the quadratojugal and the articular surface of the quadrate is absent in *spinifera*, but present in *odoratus*, *caretta*, and *serpentina*, and consequently could be considered primitive. However, based on ingroup commonality and the absence of a contact in *Mongolemys*, we consider a contact to be derived for Testudinoidea.

(12) *Contact between quadratojugal and maxilla; 0 = absent, Fig. 22; 1 = present, Figs. 23, 24 (Hirayama, 1985, 18).*

According to Hirayama (1985), among 'batagurids' a contact between the quadratojugal and maxilla is only present in *subtrijuga* and *reevesii*. We did not find a contact in our specimens of *reevesii*, but confirm its presence in *subtrijuga*.

Gaffney and Meylan (1988) listed a contact between the quadratojugal and maxilla as a synapomorphy for Platysternina {*megacephalum* + '*Chelydropsis*'} and as an independently evolved synapomorphy for Kinosternidae, whereas Shaffer et al. (1997) noted a contact to be present in Kinosternidae, *C. insculpta*, and *megacephalum*. Our observations confirm the presence of a contact in all of these extant groups. Among testudinoids, *subtrijuga* is unique in having an extensive contact in lateral view (Fig. 23). In several 'emydids,' a contact is present on the inside of the temporal arch (*barbouri*, and *nigrinoda*; polymorphic in *geographica*, *G. oculifera*, and *texana*; Fig. 24). For now, we scored all taxa as present, regardless of whether the contact is visible in lateral view, medial view, or both. In several other 'emydid' taxa, the bones closely approach one another, but do not actually meet, on the inside of the temporal arch (*alabamensis*, *ernsti*, *flavimaculata*, *gibbonsi*, *kohnii*, *P. nelsoni*).

Polarity: A contact is present between the quadratojugal and maxilla in *odoratus*, but absent in *spinifera*, *caretta*, *serpentina*, and *Mongolemys*. We consider the presence of a contact to be derived for Testudinoids.

(13) *Medial contact of the maxillae along the anterior margin of the jaw; 0 = absent, Figs. 25, 26; 1 = present, Fig. 27 (modified from Hirayama, 1985, 20; McCord et al., 1995, 2; Yasukawa et al., 2001, 10).*

In most testudinoids, the anteromedial ends of the maxillae are separated medially by the premaxillae along the anterior margin of the jaw (Fig. 25). Hirayama (1985) noted that the maxillae have a medial contact in some 'batagurids,' which was confirmed by McCord et al. (1995) and Yasukawa et al. (2001) for *spengleri* and several other species that they included in the genus *Geoemyda*. We found a broad medial contact of the maxillae in *spengleri* and *annulata* (Fig. 27). In some species, the maxillae approach one another along the ventral rim of the nasal opening (e.g., *amboinensis*, *mouhotii*, *pulcherrima*, *crassicollis*), but a well-developed contact is never present (Fig. 26).

Polarity: The maxillae do not meet medially along the anterior margin of the jaw in *odoratus*, *caretta*, *serpentina*, and *Mongolemys*. A medial contact is present in *spinifera* but only along the ventral border of the external nares. We consider a medial contact along the anterior margin of the jaw to be the derived condition within Testudinoidea.

(14) *Size of the foramen orbito-nasale; 0 = small, less than 1/6 of orbit length, Figs. 28, 29; 1 = large, more than 1/6 of orbit length, Fig. 30 (modified from Hirayama, 1985, 33; Gaffney and Meylan, 1988, F9.3, F10.2, G10.3, H11.1, H16.3; Crumly, 1982, 25; Crumly, 1994, 12).*

We were cautious when first approaching this character due to the inconsistent usage and definition of

'small' and 'large' by various authors. However, after assessing the size of this foramen based on its size relative to the length of the orbit, we were surprised to see that we were able to reproduce Hirayama's (1985) scoring for the 'batagurids' without too many difficulties. In contrast, our initial observations of tortoises were in stark contrast to those of Crumly (1982, 1985, 1994) and Gaffney and Meylan (1988). This may be due to the thin nature of the palatine of many tortoises, and the relative ease with which that part of the palate can be damaged during skeletal preparation and handling. Furthermore, the foramen becomes progressively more closed with increased ontogenetic age (Crumly, 1982). We encountered similar problems in attempting to score *reticularia* and *blandingii*. Because we deem this character to be potentially useful for helping to resolve phylogeny within 'batagurids' and 'emydids,' we decided to score all testudinoids with delicate palatines (i.e., all tortoises, *reticularia*, and *blandingii*) as 'unknown.' We acknowledge that our redefinition of the character is still subjective and somewhat problematic, but using this definition we were able to unambiguously score all the ingroup taxa we examined.

Polarity: The foramen orbito-nasale is large in *serpentina*, *odoratus*, and *spinifera*, but small in *caretta*. We consider presence of a large foramen orbito-nasale to be the derived condition within testudinoids, because the foramen is small in *Mongolemys*.

(15) *Contact between maxilla and vomer; 0 = present, Fig. 31; 1 = absent, vomer separated from the maxilla by the premaxilla, Fig. 32 (Hirayama, 1985, 31; Crumly, 1982, 21; Yasukawa et al., 2001, 14).*

We generally agree with previous scorings for this character (Hirayama, 1985, Crumly, 1982, Yasukawa et al., 2001). We confirm the absence of a contact in *amboinensis* and *pulcherrima*, but our scoring differs slightly for those taxa that Hirayama (1985) coded as 'intermediate apomorphic,' a character state that we interpret as polymorphism. Of those taxa that Hirayama (1985) and Yasukawa et al. (2001) scored as intermediate (*flavomarginata*, *caspica*, *annulata*), our sample size is too small to confirm whether both character states are present. We consequently follow these authors by scoring those taxa as polymorphic.

Polarity: A contact between the maxilla and vomer is present in all outgroups. The loss of this contact is derived for testudinoids.

(16) *Size of the foramen palatinum posterius; 0 = large, Fig. 33; 1 = small, Fig. 34 (modified from Hirayama, 1985, 22; Gaffney and Meylan, 1988, F2.2, F6.1; McCord et al., 1995, 4; Yasukawa et al., 2001, 12).*

Our characters 16 and 17 were published originally by Hirayama (1985) as one character that combined two morphological features: the size of the foramen palatinum posterius (f.p.p.) and participation of the pterygoid in the margin of the f.p.p. Although four possible combinations of these features are logically possible, only two were originally included (participation present, f.p.p. large; participation absent, f.p.p. small). Gaffney and Meylan (1988) also used this character within 'emydids,' but their character applied only to the exclusion of the pterygoid from the f.p.p. We decided to subdivide Hirayama's (1985) character into one character that describes the size of the f.p.p. and a second that addresses the position of the pterygoid relative to the f.p.p.

We found no difficulty in identifying the f.p.p. as 'large' or 'small,' (Figs. 33 and 34, respectively), and no ambiguous condition was encountered. Because our character definition only includes two character states, our scorings do not reflect those of other workers with a more limited target group (e.g., McCord et al., 1995). In juveniles the f.p.p. tends to be larger, but during later ontogenetic stages the f.p.p. is slowly reduced in size.

Polarity: The f.p.p. is small in *odoratus*, *spinifera*, and most pleurodires; it is absent in *caretta*, but is large in *serpentina* and *Mongolemys*. We consider a small f.p.p. to be the derived state.

(17) *Position of the pterygoid relative to foramen palatinum posterius (f.p.p.); 0 = pterygoid situated posterior to the f.p.p., Fig. 33; 1 = pterygoid situated posterior to the f.p.p., but sends a process anterior and lateral to the f.p.p., Fig. 34.*

Our survey of testudinoids indicated that reliable assessment of participation of the pterygoid in the f.p.p. may be difficult because many species show an ontogenetic change in configuration of this part of the palate. In juveniles, the f.p.p. typically includes the pterygoid in its posterior margin. During later ontogenetic stages the pterygoid is excluded. In spite of this, it appears that the relative position of the pterygoid tends to stay constant during ontogeny.

Polarity: The anterior end of the pterygoid is situated posterior to the f.p.p. in *odoratus*, *serpentina*, most pleurodires, and *Mongolemys*, but is situated lateral to the f.p.p. in *spinifera*. We consider a posterior position to be primitive for Testudinoidea.

(18) *Epipterygoid participation in the trigeminal foramen; 0 = absent, Fig. 35; 1 = present, epipterygoid clearly separates the parietal and pterygoid in lateral view, Fig. 36.*

The anteroventral rim of the trigeminal foramen of most testudinoid turtles is formed by the parietal and pterygoid. The epipterygoid commonly comes close to the foramen, but does not form part of it. In *spengleri*

and *mouhotii*, the epipterygoid consistently participates in the margin of the trigeminal foramen thus separating the parietal and pterygoid, at least in lateral view.

Polarity: The epipterygoid forms part of the anteroventral rim of the trigeminal foramen in the majority of outgroups, with the exception of pleurodires that lack a definitive ossified epipterygoid (Gaffney, 1979). The condition is unclear for *Mongolemys*. However, within the ingroup we found this character only in the seemingly rather specialized turtles *spengleri* and *mouhotii*. We consequently consider its presence to be secondarily derived.

(19) *Vomerine foramen; 0 = absent, Fig. 37; 1 = present, Fig. 38 (Gaffney and Meylan, 1988, H4.1; Crumly, 1994, 15).*

The vomerine foramen (= anteromedial vomerine aperture of Crumly, 1982 and 1994 [in part]) is a small opening that pierces the vomer along the midline just posterior to the foramen praepalatinum (Bramble, 1971). The presence of a vomerine foramen was noted in *agassizii* and *berlandieri* by Bramble (1971), and was used by Gaffney and Meylan (1988) to unite various species currently placed in *Gopherus* as a clade. Its irregular presence in *elegans*, *elongata*, *chilensis*, and *radiata* was reported by Crumly (1982). Specimens in our sample enable us to confirm its presence in *agassizii*, *berlandieri*, and *chilensis*.

Polarity: The vomerine foramen occurs in only a few 'testudinids' and it is absent in all outgroups. Its presence is considered derived for Testudinoidea.

(20) *Development of the foramen praepalatinum as a canal (canalis praepalatinum) that is concealed by a bony secondary palate in ventral view; 0 = absent, Fig. 39; 1 = present, Fig. 40 (modified from Hirayama, 1985, 24).*

In most testudinoids, the foramen praepalatinum is a small opening that connects the nasal cavity with the roof of the oral cavity (Fig. 39). However, in a number of taxa with extensively developed secondary palates, the anterior nasal artery passes through an elongated canal that is concealed in ventral view by the bony secondary palate (e.g., *baska*, *tentoria*, *petersi*; Fig. 40). We refer to this structure as the canalis praepalatinum. Our scorings are fully consistent with those of Hirayama (1985).

Polarity: The foramen praepalatinum is absent in *spinifera* (Gaffney, 1979) and *caretta* (Nick, 1912), and is developed as a true foramen that is exposed in ventral view in *odoratus*, *serpentina*, and *Mongolemys*. The development of a canalis praepalatinum is considered the derived condition within Testudinoidea.

(21) *Contact between pterygoid and basioccipital; 0 = present, Fig. 41; 1 = absent, Fig. 42 (modified from Gaffney and Meylan, 1988, F1.1, F10.3, H18.3; Crumly, 1994; Shaffer et al., 1997, 103).*

Two of the most often-cited characters that purportedly help to distinguish the 'Emydidae' from the 'Bataguridae' are the batagurine process and the contact between the pterygoid and the basioccipital (McDowell, 1964). Both traits are commonly combined as one character (e.g., Gaffney and Meylan, 1988) and even seem to have been confused with one another (e.g., Mlynarski, 1976; Shaffer et al., 1997). The batagurine process is a poorly-defined feature that, in McDowell's original usage (1964) appears to consist of a lateral process of the basioccipital that floors the recessus scalae tympani. Many testudinoid species (including non-'batagurines') have a laterally-projecting process of the basioccipital; it may or may not floor the recessus scalae tympani, but it is often obscured from view in articulated specimens. When disarticulated material is examined, a broader distribution of this feature (assuming it is interpreted as we have done above) across testudinoids is revealed.

Within Testudinoidea, the pterygoid commonly sends a process posteriorly and contacts the basioccipital just lateral to the basisphenoid. This character appears to be absent in most 'emydids,' but is present in *terrapin* and those species that are currently attributed to *Graptemys* (Gaffney and Meylan, 1988). We noticed a strong ontogenetic component to this character within 'emydids.' The pterygoid is commonly rather short during younger ontogenetic stages, but finally reaches the basioccipital in later stages. For instance, among our specimens of *terrapin, orbicularis*, and *texana,* the pterygoid does not contact the basioccipital in younger individuals, but a clear contact is present in adults. We score such species as polymorphic, but note that ontogenetically influenced polymorphisms are not well explored in turtles.

Among 'batagurids,' we noted a similar pattern. Contrary to general belief we were not able to observe a contact between the pterygoid and the basioccipital in all taxa traditionally classified in this group (e.g., *trijuga*, *pulcherrima, sinensis*). As with the 'emydids,' there seems to be an ontogenetic effect in which younger specimens tend not to have a contact. Where recognized, we scored these species as polymorphic.

We found much conflicting data regarding the distribution of this character among tortoises (Crumly, 1982, 1985, 1994; Gaffney and Meylan, 1988). Among the specimens we examined, we note the complete absence of a contact only in *graeca*; polymorphisms were observed in *polyphemus* and *horsfieldi*. Again, an ontogenetic component is apparent.

Polarity: A contact between the pterygoid and

basioccipital is present in all outgroups. Its absence is considered to be derived.

(22) *Contact of the pterygoid with the articular facet of the quadrate; 0 = absent, Fig. 43; 1 = present, Fig. 44 (Hirayama, 1985, 38).*

According to the data matrix published by Hirayama (1985) he only observed this contact in *reevesii*, however, in his tree (fig. 2) the contact is mapped as an autapomorphy of *subtrijuga*. We confirm the presence of a contact between the posterior process of the pterygoid and the articular surface of the quadrate in *subtrijuga*. It is the only taxon we examined that displays the derived condition.

Polarity: A contact between the pterygoid and the articular surface of the quadrate is absent in all outgroups and the vast majority of the ingroup. We consider its presence to be derived.

(23) *Closure and depth of the incisura columella auris; 0 = absent, incisura is open, Fig. 44; 1 = present, incisura closed, Fig. 45 (Crumly, 1985; Gaffney and Meylan, 1988, H1.3).*

The incisura columella auris is a notch that is formed by the quadrate and that holds the stapes and eustachian tube (Gaffney, 1972). In a number of turtles, the incisura closes to fully surround the stapedial shaft (Gaffney and Meylan, 1988). Within testudinoids, the incisura evidently is closed in most tortoises (Crumly, 1985). We are able to confirm the presence of such a closed incisura in all 'testudinids' we examined with the exception of one specimen of *kleinmanni* (CAS 228431), the smallest of the species now classified in *Testudo*. In a number of 'batagurids' and 'emydids' the incisura commonly is very narrow and even appears to be closed, however, a closer look under the microscope combined with a probing needle reveals that this apparent closure is produced by dry tissues that remain in this area in many articulated skulls. The only 'batagurid' for which we sometimes found a closed incisura is *N. platynota*; in that species the quadrate does not fuse together forming a solid ring behind the incisura, but this is also the case for many tortoises (e.g., some *belliana*, *emys*, some *homeana*, some *kleinmanni*). In some cases, the polymorphism we noted (e.g., in *belliana* and *homeana*) appears to be a result of ontogenetic age, with older individuals displaying a greater degree of fusion at the posterior part of the incisura.

Polarity: The polarity of this character is somewhat ambiguous, because the incisura columella auris is closed in *serpentina* and *spinifera*, but open in *caretta* and *odoratus*. We conclude that its presence is derived within testudinoids because it is absent in *Mongolemys*.

Mandible

(24) *Angular contribution to the sulcus cartilaginis Meckelii; 0 = present, the angular contributes to the sulcus and is as long or longer than the prearticular, Fig. 47; 1 = absent, the angular is shorter than the prearticular, Fig. 48 (modified from Gaffney and Meylan, 1988, F1.4).*

A broad contact of the angular with Meckel's cartilage was used by McDowell (1964) to characterize the 'Emydinae' and later used by Gaffney and Meylan (1988) as a synapomorphy to unite the same grouping. As it was originally worded, this character is difficult to observe in its literal sense for most museum specimens, because the Meckel's cartilage usually is not present in modern and fossil skeletal specimens. We suggest that the spirit of McDowell's (1964) character can be evaluated by examining the participation of the angular in the sulcus cartilaginis Meckelii. We confirm that a small to broad angular contribution is present in all 'emydids' with the exception of *rubriventris*. In most 'batagurids,' the angular is a short bone that does not participate in the sulcus and barely spans half the distance the prearticular does. However, a small but clear contribution to the sulcus is present in an eclectic group comprised of *baska*, *dentata*, *thurjii*, *punctularia*, and some *grandis*. We were not able to carefully evaluate potential polymorphisms in these taxa.

Polarity: An angular contribution to the sulcus cartilaginis Meckelii is present in all cryptodiran outgroup taxa. We consider is absence to be derived.

(25) *Contact between surangular and dentary; 0 =simple contact, Fig. 49; 1 = strongly interdigitated suture, Fig. 50 (Crumly, 1982, 12; Crumly, 1985; Gaffney and Meylan, 1988, H6.1).*

In most testudinoids, the surangular and dentary meet along the lateral side of the mandible in a simple, overlapping contact. According to Crumly (1982, 1985), this contact is stabilized through a finger-like process of the surangular that interdigitates with the dentary in all tortoises except *emys*, *impressa*, and those species he classified in *Gopherus*. We confirm the absence of this character in *agassizii*, *berlandieri*, *emys*, *impressa*, and *polyphemus*, but also did not observe it in *areolatus*.

Polarity: An interdigitated contact between the surangular and dentary is absent in all outgroups and the majority of the ingroup. We consider its presence to be derived.

(26) *Height of the processus coronoideus; 0 = as high as dentary, Fig. 51; 1 = rising significantly above the dentary, Fig. 52 (modified from Hirayama, 1985, 45).*

The coronoid of most turtles is a small bone that produces a minor knobby projection that rises only little

above the adjacent dentary, if at all. According to McDowell (1964) and Hirayama (1985) the coronoid is larger and rises moderately above the dentary in *borneensis* and *crassicollis*, and in *reevesii* and *subtrijuga* the coronoid is very large and produces a robust process that sits high above the dentary. We confirm these observations, however, we were also able to observe moderately developed coronoid processes in *kachuga* and *tentoria*. Among 'emydids,' we also observed moderately developed coronoids in *barbouri*, *ernsti*, *flavimaculata*, *geographica*, *gibbonsi*, *kohnii*, and *terrapin*. Unlike Hirayama (1985), we only utilize one derived character state, because it is difficult to objectively measure and discretize the relative height of the coronoid among turtles.

Polarity: The coronoids of *caretta*, *serpentina*, and *odoratus* are small and do not rise above the dentary, but the coronoid of *spinifera* is well developed and forms a moderate process. The lower jaw is not described for *Mongolemys*. We consider well-developed coronoids to be derived within testudinoids.

(27) *Foramen dentofaciale majus; 0 = small, Fig. 53; 1 = large and situated within a large lateral fossa, Fig. 54 (Hirayama, 1985, 47).*

The foramen dentofaciale majus of most testudinoids is a small opening that is situated on the lateral side of the mandible, just ventral and slightly anterior to the coronoid. The foramen dentofaciale majus is greatly enlarged in *thurjii* and *ocellata* and is situated at the anterior end of an expanded lateral fossa (Hirayama. 1985). We confirm the enlargement in those taxa, and further note its presence in *petersi*.

Polarity: The foramen dentofaciale majus is small in all outgroups and the vast majority of the ingroup. Its presence is considered to be derived.

Triturating Surfaces

(28) *Participation of palatine in the triturating surface of the upper jaw; 0 = absent, Fig. 55; 1 = present, Figs. 56, 57 (Hirayama, 1985, 26; Gaffney and Meylan, 1988, F2.1).*

In some testudinoids, the palatine has a ventrolateral maxillary process that participates in the triturating surface of the upper jaw. The degree of participation varies among taxa, and within some species. A clear and extensive participation is present in *barbouri*, *ernsti*, *geographica*, *gibbonsi*, *petersi*, *rubriventris*, *scripta*, *terrapin*, *texana*, and *versa*. It is weakly developed in *hamiltonii*, *ocellata*, *G. oculifera*, *ouachitensis*, *reevesii*, *subtrijuga*, and some individuals of *baska*.

Participation was used by Gaffney and Meylan (1988) to unite *Terrapene* spp., *blandingii*, *guttata*, *G. insculpta*, *marmorata*, *muhlenbergii*, and *orbicularis* as a clade within the 'Emydidae.' In our observations, however, this participation also is absent among other 'emydids' such as *flavimaculata*, *kohnii*, *nigrinoda*, *picta*, and *reticularia* (we were not able to evaluate adequately the potential for polymorphism in these taxa). In addition, it appears that the absence of a palatine participation represents the plesiomorphic state for testudinoids, thus eliminating its value for diagnosing monophyletic groups.

Polarity: The palatine does not participate in the triturating surface of *spinifera*, but does so in *odoratus*, *caretta*, and *serpentina*. The palatine does not participate in the triturating surface of *Mongolemys* and only occurs in Testudinoids with highly derived secondary palates. We consequently consider the participation of the palatine in the triturating surface to be derived within testudinoids.

(29) *Participation of the vomer in the triturating surface of the upper jaw; 0 = absent, Figs. 56, 57, 58; 1 = present, Fig. 59 (Hirayama, 1985, 25).*

The triturating surface is the grinding surface of the jaw. In most turtles, it is formed on the upper jaw predominantly by the maxilla and premaxilla. However, in turtles with extensive secondary palates the vomer may also participate. In *texana*, the vomer may have a ventral projection that barely separates the maxillae in the midline, but it does not participate in the triturating surface proper because it sits in a dorsal concavity within the palate (Fig. 56). Our scorings differ from those of Hirayama (1985) for *mouhotii* (which Hirayama scored as "intermediate apomorphic" and we score as absent because it does not have a secondary palate) and *subtrijuga* (in our specimens the vomer does not descend to the palatal surface, but this species may be polymorphic). This character is polymorphic in *barbouri*.

Polarity: Because the vomer does not participate in the triturating surface of *odoratus*, *spinifera*, *caretta*, *serpentina*, and *Mongolemys*, its participation is considered to be the derived condition for Testudinoidea.

(30) *Presence and number of lingual ridges of the triturating surfaces of the upper and lower jaws; 0 = no lingual ridges present, Fig. 60; 1 = one lingual ridge present, Figs. 61-62; 2 = two lingual ridges present (modified from Hirayama, 1985, 29, 44; Gaffney and Meylan, 1988, F7.2, F9.1)*

Most turtles lack lingual ridges on their triturating surfaces (Fig. 60), but one or two such ridges are developed in a number of testudinoids (Figs. 61-62). These ridges run parallel to the labial surface of the maxilla and dentary, and typically do not meet their counterpart on the midline. They are not necessarily a continuous structure (Fig. 61), and may be divided into several com-

ponents. In some cases, an extensive ridge-like structure can create the appearance of an additional ridge at the extreme lingual margin of the maxilla bordering the internal nares; however, we consider these to be the thickened rim of the internal nares rather than an additional ridge. Among 'batagurids' and 'emydids,' one lingual ridge is present in *alabamensis*, *borneoensis*, *decorata*, *kachuga*, *P. nelsoni*, *ocellata*, *petersi*, *rubriventris*, *scripta*, *sinensis*, *tentoria*, *texana*, and *thurjii*. Two lingual ridges are developed in *baska*. We found lingual ridges in all tortoises we examined except *erosa*, *belliana*, and *homeana*.

Hirayama (1985) originally scored this character as two separate characters, one for the mandible and one for the maxilla. In our observations, the triturating surface of the lower jaw closely mimics that of the upper jaw, creating an occlusal surface that closely reproduces the function of cusps in mammalian cheek teeth. Both characters were scored in parallel in Hirayama's matrix, and we see no reason to consider them independent.

Polarity: All outgroups lack lingual ridges on the triturating surfaces. We consequently consider their presence to be derived.

(31) *Well-developed serrations on labial or lingual ridges of the triturating surfaces of the upper and lower jaws; 0 = absent, Fig. 60; 1 = present, Fig. 61 (modified from Hirayama, 1985, 21, 27, 41, 43, 46; Gaffney and Meylan, 1988, F9.2; Yasukawa et al., 2001, 11).*

Well-developed serrations on the lingual and labial ridges of the upper and lower jaws are developed in several 'batagurids' and 'emydids'. A number of tortoises and other 'batagurids' (e.g., *carbonaria*, *pardalis*, *sulcata*, *annulata*, and *areolata*) exhibit serrations on their ramphothecae, but unlike the bony, tooth-like serrations of *borneoensis*, *thurjii*, *petersi*, or *texana*, these crenulations are weakly developed, leaving very little or no trace of serrations on the underlying bone. In comparison to those taxa with well-developed serrations, it very difficult to establish a consistent scoring system for taxa with fine crenulations, because many specimens will not exhibit any serrations, probably due to wear of the ramphothecae. Unlike Hirayama (1985) and Yasukawa et al. (2001) we scored all taxa with such weak serrations as absent.

Unfortunately, even in those taxa with well-developed serrations, the serrations are not always evenly developed on all ridges. We consequently combined all of Hirayama's (1985) characters relating to serrations into one character. Because serrations commonly occur on all available ridges, this treatment will also help to avoid unconsciously weighting the presence of serrations with up to five characters. In those taxa that have them, the ridges themselves often have very different morphologies; this character needs to be critically reevaluated with adequate sample sizes for the relevant taxa.

Polarity: All of our outgroup taxa and the majority of the ingroup taxa lack strong serrations. We interpret their presence to be derived.

(32) *Median ridge or sulcus of the triturating surface of the upper jaw; 0 = both structures absent, Fig. 60; 1 = median ridge present, Fig. 62; 2 = median sulcus present, Fig. 63 (modified from Hirayama, 1985, 30; Crumly, 1985, 1994, 4; Gaffney and Meylan, 1988, H3.1).*

In a number of testudinoid turtles with partially developed secondary palates and lingual ridges, additional structures are formed along the midline of the upper jaw that typically correspond to reciprocal structures of the lower jaw. The upper jaw of *petersi* is characterized by a narrow sulcus (Fig. 63) and the mandible exhibits a low median ridge. On the other hand, in *baska*, *borneoensis*, *thurjii*, *kachuga*, *agassizii*, *berlandieri*, and *polyphemus*, a ridge runs along the midline (Fig. 62), which typically corresponds to a sulcus in the lower jaw. An incipient ridge also was reported in *emys* (Crumly, 1994), but we were not able to confirm this on the specimen available to us.

Polarity: A median ridge is absent in all outgroups and the vast majority of the ingroup. Its presence is considered to be derived.

(33) *Posterior extension of the lower triturating surface behind the symphysis of the dentary; 0 = absent, Fig. 64; 1 = present, Fig. 65 (Hirayama, 1985, 42; Gaffney and Meylan, 1988, G5.2).*

In several 'batagurids,' the triturating surface of the dentary forms a shelf along the midline that extends so far posteriorly that the symphysis cannot be seen when the mandible is observed in dorsal view (McDowell, 1964). Our scorings fully agree with those of Hirayama (1985) for the 'Bataguridae,' but we disagree with Gaffney and Meylan (1988) who asserted that this character also occurs in some 'Emydidae.' Admittedly, several species currently placed in the genera *Graptemys*, *Pseudemys*, and *Trachemys* have greatly expanded triturating surfaces of the dentary, but in all of the specimens available to us, the symphysis is always visible in dorsal view.

Polarity: An extended triturating surface of the dentary does not occur in any outgroup taxon. We consider its presence to be derived.

Carapace

(34) *Carapace strongly tricarinate in adult; 0 = absent, Figs. 66, 67; 1 = present, Fig. 68 (modified from*

Hirayama, 1985, F; McCord et al., 1995, 10; Yasukawa et al., 2001, 24).

Three distinct carapacial ridges are present in the adults of *reevesii*, *hamiltonii*, *spengleri*, *subtrijuga*, *trijuga*, and *mouhotii*. We cannot replicate Hirayama's (1985) placement of this character as an autapomorphy in *hamiltonii*. In our observations, the carinae in *hamiltonii* are not better developed than in some other taxa. In fact, they are more weakly developed than those in *mouhotii* (Fig. 68). Because keels are present in the young and subadults of such taxa as *crassicollis* (Fig. 67), *mutica*, and *sinensis*, but disappear with age, and because we were not able to observe the juveniles of most species, we restricted this character to those species that exhibit well-developed tricarinae as adults. Three keels were reported to be present in the adults of *dentata* (McCord et al., 1995), but we cannot confirm this (tricarinae are not present on our younger specimens).

Polarity: Tricarinae are absent in our outgroup species (*caretta*, *odoratus*, *serpentina*, *spinifera*, *gibba*, *siebenrocki*, *subglobosa*, and *subrufa*), but do appear occasionally in some of their close relatives, such as *scorpioides*, *temminckii*, and *fimbriatus*. We consider the presence of tricarinae to be derived within Testudinoidea.

(35) *Significant serration of the posterior peripherals; 0 = absent, Fig. 66; 1 = present, Fig. 68 (modified from Hirayama, 1985, D; McCord et al., 1995, 11; Yasukawa et al., 2001, 23).*

We generally agree with previous observations reported for this character (Hirayama, 1985). However, because the carapace rim is at least slightly serrated in almost all turtles, we rephrase the character definition to include only significantly serrated posterior peripherals as found, for example, in *crassicollis*, *dentata*, *grandis*, *mouhotii*, *N. platynota*, and *spengleri*. Among the 'emydids' and 'testudinids,' the peripherals of *barbouri*, *erosa*, *flavimaculata*, *geographica*, *homeana*, *kohnii*, *nigrinoda*, *oculifer*, *G. oculifera*, *pseudogeographica*, and *versa* also are serrated. It is important to note that our scores are based on the peripheral bones; the amount of carapacial serration greatly depends on the presence or absence of the marginal scutes in the specimens used, because the scutes greatly accentuate the amount of serration, if present. We find no conflict with the codings of McCord et al. (1995) and Yasukawa et al. (2001).

Polarity: Serrated posterior peripherals are present in *caretta*, but absent in *odoratus*, *serpentina*, and most pleurodires. However, due to ingroup commonality and its absence in taxa placed within "Lindholmemydidae" we conclude that its presence is derived.

(36) *Carapace of adult tectiform in cross-section with a strong posterior projection on the third vertebral scute; 0 = absent, Fig. 69; 1 = present, Fig. 70 (Hirayama, 1985, N).*

According to Hirayama (1985), this character only occurs in *tecta* and *tentoria*. For our sample, we were able to confirm its presence in *tecta* and *tentoria* and also observed it in *barbouri* (*barbouri* and other species now classified in *Graptemys* may be sexually dimorphic for this character). The descriptive term 'tectiform' is somewhat problematic, because any turtle shell can be considered 'roofed' (Fig. 69). We regard a carapace as tectiform if its sides are more-or-less flat and meet along the midline at a rather sharp angle (Fig. 70). Many testudinoids, and notably those 'emydids' currently classified within *Graptemys*, have a somewhat tectiform carapace as juveniles, but that morphology typically is lost in the adults.

Polarity: Because all outgroups and the majority of the ingroup do not have a tectiform carapace, we consider its presence to be derived.

(37) *Shape and orientation of the second neural; 0 = second neural hexagonal, short sides positioned anteriorly, Fig. 71; 1 = second neural hexagonal, short sides positioned posteriorly, Fig. 72; 2 = second neural octagonal, Fig. 73 (modified from Hirayama, 1985, G; Yasukawa et al., 2001, 25).*

(38) *Shape and orientation of the third neural; 0 = third neural hexagonal, short sides positioned anteriorly, Fig. 71; 1 = third neural hexagonal, short sides positioned posteriorly, Fig. 72; 2 = third neural square, Fig. 74; 3 = third neural octagonal, Fig. 75 (modified from Hirayama, 1985, G; Yasukawa et al., 2001, 25).*

Originally, Hirayama (1985) only discussed the orientation of the neurals in general, which is fully sufficient for his 'batagurid' ingroup, because almost all individuals exhibit his two suggested character states. However, in most tortoises the second and/or third neurals are not hexagonal, but rather are square or octagonal, making it impossible to assign them to one of Hirayama's (1985) character states. We consequently split Hirayama's original character into two characters, restricted their application to the second and third neural, and added additional character states.

Our observations generally agree with those of Hirayama (1985) and Yasukawa et al. (2001) for 'batagurids,' with the exception of *annandalei* in which we found the short side of the second and third neurals to be positioned anteriorly, and not posteriorly as was indicated by Hirayama (1985).

Polarity: The short side of the second and third neural bones faces posteriorly in *odoratus* and *spinifera* but

anteriorly in *caretta*. The shape of the second and third neurals is extremely variable in *serpentina*. However, in *Lindholmemys* and *Mongolemys* the short side of the second and third neurals is positioned anteriorly. We consider that condition to be primitive for Testudinoidea.

(39) *Medial contact of the seventh and/or eighth costal bones; 0 = absent, Fig. 76; 1 = present, Fig. 77 (Hirayama, 1985, V; Yasukawa et al., 2001, 26).*

In some testudinoid turtles, the posterior costal bones meet along the midline due to the reduction of the posterior neural elements. The original character definition provided by Hirayama (1985) and Yasukawa et al. (2001) was worded to indicate a contact between the seventh *and* eighth costal bones among some 'batagurids.' We are unable to reproduce their results if the character definition is taken literally. For example, in all our specimens of *amboinensis* and *galbinifrons,* the eighth costals meet on the midline, but the seventh costals do not. However, if the character definition is modified to include any contact of the seventh or eighth costals, our results are concordant with those of Hirayama (1985) and Yasukawa et al. (2001). In addition to the Asian box turtles, we report a medial contact of the posterior costals in *baska*, *carolina*, *coahuila*, *T. nelsoni*, *T. ornata* and *rubida*.

Polarity: A medial contact of the seventh and/or eighth costals is absent in *serpentina*, but present in *spinifera*, *caretta*, many kinosternids, and many pleurodires. Although a composite reconstruction of a putative "lindholmemydid" from the Early Cretaceous of Japan was illustrated with the seventh costals in contact at the midline (Hirayama et al., 2000, fig. 11), such a contact is absent in other specimens of *Lindholmemys* and *Mongolemys*. Its presence within testudinoids is predominantly in the highly derived box turtles, and we conclude that its presence is derived for Testudinoidea.

(40) *Cervical scute; 0 = present, Fig. 78; 1 = absent, Fig. 79 (modified from Crumly, 1985, 1994, 34; Gaffney and Meylan, 1988, H5.2, H10.1; Shaffer et al., 1997, 41).*

The presence and shape of the cervical scute is used commonly to determine phylogenetic relationships within tortoises. According to Crumly (1985) the cervical scute is very narrow or absent in all tortoises except *agassizii*, *berlandieri*, *emys*, *flavomarginatus*, *impressa*, and *polyphemus*. We generally agree with these observations, but when this character is applied to all testudinoids intraspecific variation is so great that the character becomes essentially useless. We consequently limit our scoring to the mere presence or absence of the cervical scute. We confirm the observations of Gaffney and Meylan (1988) that this scute is absent in *carbonaria*, *chilensis*, *elegans*, *nigra*, *pardalis*, and *sulcata* and additionally code *homeana* and *erosa* as polymorphic.

Polarity: The cervical scute is present in all cryptodiran outgroups that have scutes on their carapace. We consider its absence to be derived.

(41) *Number of vertebral scutes; 0 = five, Fig. 80; 1 = six or more, Fig. 81 (Hirayama, 1985, P).*

We confirm Hirayama's (1985) observation that there are at least six vertebral scutes in *N. platynota*. Additional scutes occasionally occur in other species, but are best considered abnormalities; they typically lack the symmetrical associations with adjacent pleural scutes seen in *N. platynota*.

Polarity: All testudinoids, except for *N. platynota,* have five vertebral scutes. We consider the presence of six scutes to be derived.

(42) *Position of the anterior sulcus of the fourth vertebral scute; 0 = sulcus lies on the fifth neural, Fig. 82; 1 = sulcus lies on fourth neural, or on the suture between the fourth and fifth neural, Fig. 83; 2 = sulcus lies on the sixth neural, or on the suture between the fifth and sixth neural, Fig. 84 (modified from Hirayama, 1985, L+M).*

(43) *Position of the posterior sulcus of the fourth vertebral scute; 0 = sulcus lies on the eighth neural, or on the homologue of the eighth neural, if the seventh is reduced (e.g., in most tortoises), Fig. 85; 1 = sulcus lies on the seventh neural, or on the suture between the seventh and eight neural, Fig. 86; 2= eighth neural absent, sulcus overlies costals that meet at the midline, Fig. 87 (modified from Hirayama, 1985, L+M).*

The size of the fourth vertebral scute was addressed with two characters by Hirayama (1985) but the total range of morphological variability in testudinoids is not encompassed by his character definitions. In most testudinoids, the fourth vertebral scute covers the posterior half of the fifth neural bone, the sixth and seventh neurals, and the anterior half of the eighth neural. A number of variations are known, and simply counting the number of neural bones covered by this scute results in problems by creating a false perception of homology. For instance, a fourth scute that partially overlies the fourth and seventh neurals and fully covers the fifth and sixth, can strictly be said also to cover four neurals, but the elements involved are only partially homologous with the common condition. We attempt to resolve these issues by establishing two new characters that preserve what we think was Hirayama's (1985) original intent, but that permit a more accurate representation of the association between the fourth vertebral scute and the underlying neural bones.

Some problems that are associated with scoring this character include the prevalence of scute abnormalities among testudinoids (e.g., Coker, 1905, 1910; Newman, 1906; Zangerl and Johnson, 1957). Specimens exhibiting such abnormalities were scored as unknown. The notable exception to this is *N. platynota*, in which a sixth, or even a seventh, vertebral scute is always present.

Polarity: Determining the polarity through outgroup relationship is somewhat difficult, because almost every outgroup exhibits a different condition, especially for the posterior sulcus. Based on ingroup commonality, and the presence of our zero state in both *Lindholmemys* and *Mongolemys*, we consider the sulci of the fourth vertebral scute to be primitively situated on the fifth and eighth neural bones.

(44) *Posterior margin of first vertebral scute significantly narrower than its anterior margin; 0 = absent, Fig. 88; 1 = present, Fig. 89 (modified from Hirayama, 1985, C).*

When originally proposed, this character was applied to a posterior constriction of all vertebral scutes (Hirayama, 1985). If strictly applied, this character is absent in all taxa, because the fifth vertebral scute never is constricted along its posterior edge relative to the anterior edge. If each scute is viewed by itself, it becomes apparent that especially the fourth vertebral scute tends to be narrowed posteriorly, as can be observed in all species now classified in the genera *Graptemys*, *Heosemys*, *Trachemys*, and *Testudo* among others. According to Hirayama (1985), posterior narrowing is limited to *crassicollis* and *borneensis* and unites them as a synapomorphy. We were able to replicate this distribution only if the character definition was restricted to the first vertebral scute, in which the posterior margin is significantly narrower than its anterior margin in those two species only. In making this change, however, this character becomes at least partly redundant with characters 45 and 47.

Polarity: Outgroup analysis reveals that posterior narrowing of the first vertebral scute is present only in *odoratus*; it is absent in *Lindholmemys* and *Mongolemys*. We regard the presence of a posterior narrowing of the first vertebral scute to be derived.

(45) *Anterior half of the first vertebral scute much narrower than posterior half, especially in adults; 0 = absent, Fig. 90; 1 = present, Fig. 91 (modified from Hirayama, 1985, R).*

We confirm the clear presence of an anteriorly narrowed first vertebral scute in *dentata* and *spinosa* as reported by Hirayama (1985), and note that *grandis* is polymorphic. Because the anterior sulcus of the first vertebral scute commonly is restricted to the nuchal bone in several other taxa, but the scute shows no anterior narrowing, we limit the original character definition to the shape of the first vertebral scute only. This peculiar morphology seems to be the result of growth that is limited to the anterior edge and the posterior half of the lateral edge of the first vertebral scute. As a consequence, this character is not apparent in juveniles, but becomes increasingly accentuated in adults.

Polarity: Anterior narrowing of the first vertebral scute is absent in all outgroups and within the large majority of the ingroup. We consider its presence to be derived.

(46) *Significant contact of the tenth marginal scute with the fifth vertebral scute; 0 = absent, Fig. 92; 1 = present, Fig. 93 (modified from Hirayama, 1985, K).*

Contact of the tenth marginal scute with the fifth vertebral scute was reported previously only in *baska*, *smithii*, *tecta*, and *tentoria* (Hirayama, 1985). We are able to confirm the presence of a very well developed contact in all but *smithii* (not seen), and we add *spinosa* to the list of species in which this contact may occur (it is polymorphic for *spinosa*; contact is present in CAS 228368, but absent in the smaller CAS 228459, so ontogenetic differences may explain the polymorphism). We also note slight contacts in some specimens of other species (e.g., *agassizii*, *borneoensis*, *carbonaria*, *homeana*, *orbicularis*, *pardalis*, and *polyphemus*), but by rewording Hirayama's (1985) original character to include only significant contact, we are able to retain what we believe was his original intent.

Polarity: Due to the absence of contact in all outgroups in which it is applicable and the predominance within the ingroup, we consider its presence to be derived.

(47) *Contact of the second marginal scute with the first vertebral scute; 0 = absent, Fig. 94; 1 = present, Fig. 95 (Hirayama, 1985, O; see also Tinkle, 1962, table 1, 'Seam A').*

According to Hirayama (1985), the first vertebral scute usually (>90%) contacts the second marginal scute in *japonica*, *leprosa*, and *caspica*. He also noted that the scutes are sometimes in contact in *N. platynota* and *bealei*. For our sample, we are able to confirm this contact as a polymorphism for *bealei*, *caspica*, *japonica*, and *leprosa*, but the contact is clearly absent in all our specimens of *N. platynota*. We also note that these scutes are sometimes in contact in *picta*, *amboinensis*, *orbicularis*, and *terrapin*. Together with all of the above, these taxa were scored as polymorphic. The only taxa to exhibit a consistently well-developed contact are *reticularia* and *blandingii*.

Polarity: A clear contact between the second marginal scute and the first vertebral scute does not exist in *caretta* or *serpentina*, but both morphologies occur in kinosternids and pleurodires. The scutes are not in contact in *Lindholmemys* and *Gravemys*, but they are in contact in *Mongolemys*. The polarity for this character is ambiguous.

(48) *Contact of the sixth marginal scute with the third pleural scute; 0 = absent, Fig. 96; 1 = present, Fig. 97 (modified from Hirayama, 1985, B; see also Tinkle, 1962, table 3, 'Seam C').*

The contact between the sixth marginal and third pleural scutes is easily enough rendered as a simple 'presence or absence' character, but this hides the range of possible morphological variation. The degree of contact can range from extensive to a condition where the two scutes just barely contact at their corners. Several taxa exhibit a condition where these scutes either barely touch or do not touch one another at their corners, but whenever several specimens were available to us, they typically turned out to be polymorphic. For this reason Gaffney and Meylan (1988) called this character 'dubious.' We scored such borderline cases as polymorphic, even if not enough specimens were available to corroborate this.

We confirm Hirayama's (1985) observations regarding the absence of a contact between these scutes in *baska*, *ocellata*, *tecta*, *tentoria*, and *thurjii*, and we add *petersi* and *spinosa* to that list. Taxa that we score as polymorphic include *annandalei*, *borneensis*, *borneoensis*, *caspica*, *crassicollis*, *grandis*, *hamiltonii*, *japonica*, *punctularia*, *reevesii*, *sinensis*, *subtrijuga*, and *trijuga*. Whereas all 'emydids' lack a contact, tortoises exhibit both character states.

The presence of a contact between the sixth marginal scute and the third pleural scute was considered by Hirayama (1985) to unite crown group 'batagurids' and 'testudinids' as a synapomorphy. Given the patchy distribution of this character, and widespread polymorphism, it seems to be of little use.

Polarity: A contact between the sixth marginal scute and the third pleural scute is absent in most outgroups. The exception is *caretta*; this is not surprising because *caretta* has five instead of four pleural scutes. We consider the presence of a contact to be derived.

(49) *Twelfth marginal scute; 0 = two present, their common sulcus only partially subdivides the pygal bone, Fig. 98; 1 = two present, but their common sulcus fully subdivides the pygal bone, Fig. 98; 2 = both twelfth marginal scutes fused along the midline, Fig. 99 (modified from Mlynarski, 1976; Crumly, 1985, 1994, 35; Gaffney and Meylan, 1988, H2.1).*

According to McDowell (1964, p. 240 and table 1 number 4) members of the 'Emydinae' can be distinguished from the 'Batagurinae' based on an incomplete subdivision of the pygal bone by the median sulcus of the posterior-most marginals. We found exceptions with *picta*, *N. platynota*, *pulcherrima*, *reevesii*, *reticularia*, and *spengleri*, which do not always clearly exhibit the pattern that would be predicted by McDowell's (1964) statement, but we note that the expression of this character will depend significantly on the shape of the pygal bone. In all tortoises except *emys* and *impressa*, the twelfth marginal scutes are fused to from a single supracaudal scute that covers the posterior part of the carapace (Crumly, 1985). For this condition, we created a third character state.

Polarity: The twelfth marginal scutes are fully separated in all outgroups that have them, and their common sulcus fully subdivides the pygal bone. The pygal bone in "lindholmemydids" is polymorphic, with the 0 state found in *Lindholmemys* and *Mongolemys*, and the 1 state in *Gravemys*. Either state 0 or state 1 is primitive for Testudinoidea; the midline fusion of the twelfth marginals is a derived feature for 'Testudinidae'.

Bridge

(50) *Sutured contact between plastron and carapace; 0 = present, plastron and carapace are tightly connected by an osseous bridge, Fig. 100; 1 = absent, plastron is attached to carapace by connective tissue, Fig. 101 (modified from Hirayama, 1985, Q; Shaffer et al., 1997, 58; Yasukawa et al. 2001, 21a).*

(51) *Presence and development of anterior buttresses; 0 = anterior buttresses absent, Fig. 102; 1 = anterior buttresses present but small, and not in contact with the first costal bones, Fig. 103; 2 = anterior buttresses long and thin and just barely in contact with the costal bones, if at all, Fig. 104; 3 = anterior buttresses well developed and in clear contact with the first costal bones, Fig. 105; 4 = anterior buttresses very large and in direct contact with the first dorsal rib, Fig. 106 (modified from Hirayama, 1985, Q; Gaffney and Meylan, 1988, A14.2; Yasukawa et al., 2001, 28).*

(52) *Presence and development of posterior buttresses; 0 = posterior buttresses absent, Fig. 107; 1 = posterior buttresses present but small, and not in contact with the costal bones, Fig. 108; 2 = posterior buttresses long and thin and just barely in contact with the costal bones, if at all, Fig. 109; 3 =posterior buttresses well developed and in clear contact with costal bones V and VI, Fig. 110; 4 = posterior buttresses well developed but only in clear contact with costal bone V, Fig. 111 (modified from Hirayama, 1985, Q; Gaffney and Meylan, 1988, A14.2, Shaffer et al., 1997, 55; Yasukawa et al., 2001, 29).*

(53) *Medially-directed pivoting process for plastral hinge developed on fifth peripheral bone; 0 = absent, Fig. 112; 1 = present, Fig. 113.*

(54) *Complete or almost complete overlap of hyoplastron/hypoplastron suture by the pectoral/abdominal sulcus; 0 = absent, Fig. 114; 1 = present, Fig. 115 (modified Gaffney and Meylan, 1988, F3.2; Burke et al., 1996, 16; McCord et al., 1995, 13; Yasukawa et al., 2001, 21b).*

In most testudinoid turtles, the plastron is attached to the carapace via a fully ossified bridge and variably developed plastral buttresses. In species with a kinetic plastron, the bridge is typically absent and the plastron is attached to the carapace via connective tissues (e.g., *amboinensis*, *blandingii*, *carolina*, *dentata*, *galbinifrons*, *mouhotii*, *orbicularis*, *T. ornata*). The original configuration of this character tied the presence of plastral kinesis to the reduction of the buttresses (Hirayama, 1985). However, within testudinoid turtles the morphology of the buttresses varies significantly and independently from plastral kinesis. We consequently split this character into three discrete characters concerned with the morphology of the bridge and the buttresses.

We also developed two new characters that pertain to the morphology of the bridge region: the presence of medially-directed processes on the fifth peripherals that act as pivots for the plastral bones during shell closure (Bramble, 1974) and a revised plastral kinesis character (Gaffney and Meylan, 1988; McCord et al., 1995) that considers plastral-kinesis to be well developed only in those taxa in which the pectoral/abdominal sulcus fully overlaps the hyoplastron/hypoplastron suture, allowing optimal movement between the two plastral lobes. Most taxa with plastral kinesis also have well-developed pivoting processes on the fifth peripherals, but notable exceptions are *orbicularis* and *N. platynota*. In *blandingii*, the process is modified into an anteroposteriorly-elongated, flattened process that extends along most or all of the length of the fifth peripheral (Fig. 113). In some specimens of *blandingii*, a similar structure is developed on the sixth peripheral as well.

Polarity: Reconstructing the basal condition for these characters within testudinoids is difficult, because all living cryptodiran outgroups do not have plastral buttresses and commonly lack osseous bridges. However, the bridge of *Gravemys*, *Mongolemys*, and *Lindholmemys* is osseous, shows no signs of kinesis, and (at least in *Lindholmemys*) the anterior and posterior buttresses are well developed and touch the costal bones. We consider that morphology to be primitive for Testudinoids.

(55) *Contact between inguinal and femoral scutes; 0 = absent, Fig. 116; 1 = present, Fig. 117 (Crumly, 1985, 1994, 42; Gaffney and Meylan, 1988, H3.3, H15.2).*

Within tortoises the complete or frequent absence of a contact between the inguinal scute and the femoral scute was used previously to hypothesize the monophyly of several smaller clades, for example {*graeca* + *hermanni* + *horsfieldi* + *kleinmanni* + *marginata* + *tornieri*} (Crumly, 1985) and {*agassizii* + *berlandieri* + *flavomarginatus* + *polyphemus*} (Gaffney and Meylan 1988). We confirm the absence of a contact in representatives of the first group, but not in the second. Among the second group (traditionally classified together in *Gopherus*) the contact is strongly reduced, but still is present. Among 'batagurids' and 'emydids,' a contact is absent in all taxa with the noteworthy exception of *hamiltonii*.

Polarity: Determining the polarity for this character is somewhat difficult because all living outgroups have an arrangement of plastral scutes that is rather different from testudinoids. However, based on ingroup commonality and the absence of a contact in the "Lindholmemydidae," we conclude that the presence of a contact between the inguinal and femoral scutes should be considered derived for Testudinoidea.

(56) *Presence of musk glands; 0 = inguinal and axillary gland present; 1 = axillary gland present only; 2 = musk glands absent (modified from Crumly, 1985).*

(57) *Presence of anterior musk duct foramina; 0 = musk glands and their foramina present, Fig. 118; 1 = musk glands present, but foramina not developed; 2 = musk glands and foramina absent (modified from Hirayama, 1985, A; Gaffney and Meylan, 1988, F1.2, F5.3; Burke et al., 1996, 20).*

(58) *Presence of posterior musk duct foramina; 0 = musk glands and their foramina present, Fig. 119; 1 = musk glands present, but foramina not developed; 2 = musk glands and foramina absent (modified from Hirayama, 1985, A; Gaffney and Meylan, 1988, F1.2, F5.3; Burke et al., 1996, 20).*

According to Hirayama (1985), the presence of musk duct foramina characterizes the paraphyletic assemblage 'Batagurinae' (sensu Hirayama, 1985, not Gaffney and Meylan, 1988). We believe the difference of opinion between Hirayama (1985) and Gaffney and Meylan (1988) regarding this character is based on failure to make clear the distinction between the presence of *musk glands* and the presence of *musk duct foramina*. Musk glands are developed in almost all extant turtles (Waagen, 1972), and we consequently agree with Gaffney and Meylan (1988) that their presence should be considered primitive for all cryptodiran turtles.

However, even though most turtles have musk glands, true musk duct *foramina* are developed only in some pleurodires (e.g., *Chelodina*, *Emydura*), some 'emydids,' and all 'batagurids,' making a monophyletic Testudinoidea (sensu Hirayama, 1985) possible. Distinct musk duct grooves are present on the anterior peripherals of Kinosternidae, and tiny foramina are sometimes associated with these (Hutchison, 1991).

Because the presence of musk glands does not necessarily result in the development of musk duct foramina, we decided to score these two characters separately. We relied on an unpublished thesis on the musk glands of turtles (Waagen, 1972) to determine the presence of musk glands for most taxa. In scoring taxa not investigated by Waagen (1972) we only recorded presence of musk glands if musk duct foramina provided positive evidence for their presence (e.g., *baska*, *bealei*, *borneensis*, *galbinifrons*, *kachuga*, *mouhotii*, *petersi*, *pulcherrima*, *spengleri*, and *tentoria*). Many tortoises, consequently, had to be scored as unknown, because they were not analyzed by Waagen (1972) and do not exhibit musk duct foramina (e.g., *elongata*, *homeana*, *horsfieldi*, and *pardalis*).

Our scoring of the musk duct foramina is derived from a combination of osteological observation and data provided by Waagen (1972). Taxa not reported to possess musk glands (Waagen, 1972) were checked for musk duct foramina, but none were found. For those species that Waagen reported as having musk glands, we sought musk duct foramina on osteological specimens. Several taxa with musk glands, but only lightly ossified bridges, do not exhibit musk duct foramina (e.g., *blandingii*, *dentata*, *flavomarginata*, *orbicularis*, and *pulcherrima*) or show an asymmetry with foramina only visible anteriorly (e.g., *N. platynota*). In taxa that possess them, the musk duct foramina are sometimes contained entirely within the peripherals (e.g., *N. platynota*), and sometimes between the peripheral and the plastral buttress (e.g., *reevesii*).

Polarity: Given the presence of musk glands in all extant outgroups (Waagen, 1972), their absence should be considered derived. Musk duct foramina are not described for "lindholmemydids" but J. H. Hutchison specifically searched for them in *Mongolemys* specimens housed at IVPP and found no trace of them. Because musk duct foramina are developed in the vast majority of the ingroup, we consider their absence to be derived for testudinoids.

Plastron

(59) *Extensive overhanging lip of the epiplastra; 0 = absent, Fig. 120; 1 = present, Fig. 121 (Gaffney and Meylan 1988, H5.1, 9.2).*

In most testudinoid turtles, the epiplastra are rather flat with a slight increase in thickness along the anterior margin. In contrast, many tortoises have strongly thickened epiplastral margins that sometimes form an overhanging lip along the interior rim of the plastron. According to Gaffney and Meylan (1988) the presence of such an overhang of the epiplastra unites all tortoises except those classified in the genera *Manouria* (Fig. 120) and *Gopherus*, with a reversal occurring in giant insular forms. We confirm this general pattern, but we note the absence of an overhang in *tornieri*. A interior overhang is absent also in all extant 'emydids' and 'batagurids,' but a small overhang is present in extinct *Ptychogaster* and *Echmatemys* (Mlynarski, 1976, figs. 78, 81), taxa generally considered to belong to either the 'Emydidae' or 'Batagurinae.'

Polarity: An overhanging lip on the epiplastra is absent in all outgroups and the majority of the ingroup. We consider its presence to be derived.

(60) *Intersection of the entoplastron by the humeropectoral sulcus; 0 = absent, Fig. 122; 1 = present, Fig. 123 (Hirayama, 1985, X; Crumly, 1985; Gaffney and Meylan, 1988, F5.1; McCord et al., 1995, 15).*

This character was used to help resolve relationships within 'batagurids' by Hirayama (1985) but we were unable to replicate his results in our analysis. We agree with Crumly (1985) that the sulcus crosses the entoplastron in at least one species classified in the genus *Indotestudo* (i.e., *elongata*), but the sulcus is at the entoplastron/hyoplastron suture in our specimen of *forsteni*. The condition in species now commonly classified in *Testudo* varies widely (e.g., the suture crosses the entoplastron in *graeca* and *horsfieldi*, but does not in *hermanni* or *kleinmanni*). We also agree with Gaffney and Meylan (1988) on their distribution of this character among the 'Emydidae,' however, our scoring for *picta*, *orbicularis*, and *blandingii* is polymorphic, because the sulcus generally runs along the suture between the entoplastron and the hypoplastra, but may barely fall on either side.

Polarity: The polarity is ambiguous if only extant taxa are considered. The plastron of most outgroups is too different from that of testudinoids to be of any use for polarizing this character. For instance, the plastron of *spinifera* lacks scutes, and that of *serpentina*, *odoratus*, and *caretta* is too heavily modified to enable a meaningful comparison. Both character states are commonly found in 'batagurids,' 'emydids,' and testudinids, making an ingroup analysis futile. The humeropectoral sulcus is distinctly posterior to the epiplastron in *Gravemys* and *Mongolemys*, so we consider an intersection of this suture with the entoplastron to be derived.

(61) *Anal notch of the plastron; 0 = present, Fig. 124; 1 = greatly reduced, Fig. 125; 2 = absent, Fig. 126 (modified from Hirayama, 1985, W; Yasukawa et al., 2001, 22).*

The plastron of most testudinoid turtles has a significant anal notch. The absence of such an anal notch for *amboinensis*, *galbinifrons*, and *flavomarginata* was reported by Hirayama (1985) and we confirm those observations. An anal notch also is absent in *belliana*, *carolina*, *coahuila*, *erosa*, *homeana*, *T. nelsoni*, and *T. ornata*. To accommodate the presence of a reduced anal notch we modify Hirayama's (1985) character by creating a third character state. A reduced anal notch is found in *blandingii*, *orbicularis*, *N. platynota*, and *reticularia*. In at least one species (*mouhotii*), a distinct anal notch is present in larger individuals, but small specimens have a reduced notch (scored as polymorphic in our matrix); this suggests that development of an anal notch may be subject to ontogenetic variation in at least some testudinoids.

Polarity: In *caretta* and *serpentina* an anal notch is not present, however, their plastra are narrow and tapered posteriorly. The fleshy plastron of *spinifera* is smooth along its posterior margin, but this cannot be observed in osteological preparations. A notch is weakly developed in at least some *Lindholmemys*, but is absent in *Mongolemys*. A notch is present in kinosternids, pleurodires, most of the ingroup, and in *Gravemys*. We conclude that its absence should be considered derived for our ingroup.

(62) *Anal scutes fused; 0 = absent, Fig. 127; 1 = present, Fig. 127 (Hirayama, 1985, Z).*

The anal scutes of adult *galbinifrons*, and *flavomarginata* are at least slightly fused, especially along their posterior medial border. We fully agree with Hirayama's (1985) treatment for this character. Anal scute fusion can be identified easily in macerated specimens (Fig. 127), because the anal scutes will not separate from one another, as will all other scutes.

Polarity: Anal scute fusion is absent in the vast majority of turtles, and is considered to be the primitive condition.

(63) *Plastral scutes with vibrant, radiating color pattern; 0 = absent, Fig. 128; 1 = present, Fig. 129 (Hirayama, 1985, S; McCord et al., 1995, 16 Yasukawa et al., 2001, 32).*

Vibrant, radiating color patterns of the plastral scutes of *dentata*, *grandis*, and *spinosa* were noted by Hirayama (1985) and McCord et al. (1995). We add *tcheponensis* to this list, as well as the 'testudinids' *geometricus* and *P. oculifera*. In our specimens, the pattern of *dentata* and *tcheponensis* is not as vibrant as in *grandis* and *spinosa*.

Polarity: Vibrant, radiated color patterns are missing in all outgroups and the majority of the ingroup. Their presence is derived.

Postcranium and Soft Tissue

(64) *Development of a suprascapula; 0 = absent; 1 = present, Fig. 130 (Gaffney and Meylan, 1988, F3.1; Burke et al., 1996, 11).*

(65) *Development of an episcapula; 0 = absent; 1 = present, Fig. 130 (Gaffney and Meylan, 1988, F4.1; Burke et al., 1996, 11).*

The presence of both a suprascapula and an episcapula apparently is limited to *blandingii* and the species currently classified in *Terrapene*. A suprascapula is also present in *orbicularis*. Both structures are involved in the locking mechanism of the anterior plastral lobe during shell closure (Bramble, 1974). These structures are difficult to verify in most osteological preparations, because they may dissociate from the scapula and be difficult to recognize, and because they may ossify only in older individuals. The specimen we dissected to illustrate these features (TNHC 62532, a *T. ornata* with carapace length of 103 mm) has a completely cartilaginous episcapula, and a predominantly cartilaginous suprascapula (Fig. 130). It is therefore much easier to confirm their presence than verify their absence. We followed Bramble's (1974) account of these structures and scored our matrix accordingly, as probably did Gaffney and Meylan (1988) and Burke et al. (1996).

Polarity: Suprascapulae and episcapulae are absent in all outgroups and the majority of the ingroup. Their presence is considered to be derived.

(66) *Shape of coracoid blade; 0 = long and narrow, Fig. 131; 1 = short and very wide, Fig. 131 (Crumly, 1985, 1994; Gaffney and Meylan, 1988, H1.7).*

The coracoid blade of all 'emydids' and 'batagurids' is an elongate bone with a narrow, short shaft and a long, wedge-shaped coracoid blade that is about two times wider than the base. In tortoises, this bone is still wedge-shaped, but relatively much shorter and with a blade that is considerably wider, typically four times the width of the base (Crumly, 1985, 1994; Gaffney and Meylan, 1988). We agree with previously published observations.

Polarity: The coracoid blade of *caretta*, *serpentina*, and *odoratus* is long and narrow and that of *spinifera* is long, but not wedge-shaped. We consider a long and narrow coracoid blade to be primitive for Testudinoidea.

(67) *Number of manual claws; 0 = five, Fig. 132; 1 = four, Fig. 133 (modified from Hirayama, 1985, J).*

Most testudinoid turtles have five manual claws with the exception of *baska* and *horsfieldi*, both of which have only four. We did not verify this character independently for all species, due to an overall lack of articulated skeletons and our limited access to pickled specimens. However, because the number of claws of the forelimbs is an easily determinable, discrete number that is regularly noted and described in the literature, we scored all remaining taxa from the comprehensive information provided by Ernst and Barbour (1989).

Polarity: Five manual claws are present in *serpentina*, *odoratus*, and almost all pleurodires (excluding species currently classified in *Chelodina* and *Hydromedusa*); three are present in *spinifera*, and two in *caretta*. The condition in "lindholmemydids" is unknown. Based on ingroup commonality, we consider five claws to be primitive for the ingroup.

(68) *Number of phalanges of manus and pes; 0 = digital formula of 2-3-3-3-3 or 2-3-3-3-2, Fig. 132; 1 = digital formula with less than 2-3-3-3-2, Fig. 133 (Crumly, 1985; Gaffney and Meylan, 1988, H1.1).*

The digital formula of most testudinoid turtles is 2-3-3-3-3 or 2-3-3-3-2. Among tortoises, the manus and pes are greatly shortened and the digital formula is typically reduced to 2-2-2-2-2 or less (Auffenberg, 1974:135-136; Crumly, 1985). Due to the dissociated nature of most of the material we viewed, we were not able to verify the digital formulae of most of the turtle taxa we included. However, when articulated hands and feet were present, we never found anything to contradict the statements made above. We scored all tortoises based on information provided by Auffenberg (1974) and Crumly (1985).

Polarity: All outgroups and the majority of the ingroup do not have a reduced digital formula. We consequently consider the reduced formula to be derived.

(69) *Webbing between digits; 0 = present, well developed, Fig. 134; 1 = absent, or at least strongly reduced, Fig. 135 (Hirayama, 1985, b).*

Due to their semi-aquatic nature, most testudinoids have well-developed webbing between the digits of their hands and feet. In more terrestrial species, however, the webbing often is reduced. Unfortunately, there seems to be a gradient in the development of webbing, from extremely well developed (e.g., *baska*, *reticularia*) to moderately developed (e.g., *dentata*, *guttata*) to virtually non-existent (e.g., *spengleri*). We nevertheless were able to reproduce Hirayama's (1985) distribution for the 'batagurids' with the exception of *grandis* and *spinosa*, which have reduced webbing (*grandis* is the only 'borderline' taxon we found, but its webbing is reduced relative to those taxa we scored as having well-developed webbing). Among 'emydids,' we note that the webbing is heavily reduced in *carolina*, *T. nelsoni*, and *T. ornata*. All tortoises lack webbing.

Polarity: All outgroups and the majority of ingroup taxa have webbed hands and feet. We consider the absence of webbing to be derived.

(70) *Sexual size dimorphism; 0 = absent; 1 = present, female much larger than male (Gaffney and Meylan, 1988, F5.2; Burke et al., 1996, 37).*

In almost every species of turtle, there is some expression of sexual size dimorphism (Berry and Shine, 1980; Gibbons and Lovich, 1990). The difference in size between the sexes can be expressed as a ratio and typically shows considerable variation depending on the population (Gibbons and Lovich, 1990). We initially tried to score this character with three character states, as done by Burke et al. (1996), differentiating between species with larger males, larger females, and equally sized sexes, but we abandoned that, because exact data are missing for most 'batagurid' taxa. We consequently only score taxa as being sexually dimorphic if females are at least 1.4 times larger than the males. Our scores are derived from Gibbons and Lovich (1990) and Ernst and Barbour (1989).

Polarity: Sexual size dimorphism is prevalent in most outgroups. In *spinifera* the female is much larger, in *odoratus* and *serpentina* the male tends to be slightly smaller, in *caretta* the sexes are of similar size. The outgroup polarity is thus ambiguous, but in the majority of the ingroup pronounced sexual dimorphism is absent.

Problematic Characters

We encountered difficulties in evaluating a number of previously used characters, and we provide some summary statements for those in this section. Most of these characters were not pursued thoroughly in our study because we were not able to understand the original descriptions, were unable recover discrete character states, or because at an early point in our investigation of the character we detected significant variation in expression of character states within taxa. In the latter case greater sample sizes or new methodological techniques (e.g., Wiens, 1995; Smith and Gutberlet, 2001) will be required to tease out a phylogenetic signal.

(A) *Frontal contribution to the supratemporal rim (Hirayama, 1985, 4).*

The anterior extent of the upper temporal emargination is difficult to define in many taxa, and is impossible to determine in those with a fully emarginated temporal region (e.g., *T. ornata*). The result is a high degree of ambiguity and a general lack of discrete character states.

(B) *Contact between postorbital and quadrate (Hirayama, 1985, 10).*

In the vast majority of ingroup taxa, there is no contact between the postorbital and the quadrate. Such a contact was observed only in *japonica* and *punctularia* by Hirayama (1985). In specimens of *japonica* available to us, we were not able to confirm this contact. CAS 228348 is a skeleton from a diseased specimen of *punctularia*. On the right side of the skull there is a possible (but only slight) contact. It is possible that the contact is actually between the postorbital and the quadratojugal (Fig. 136). We also found a minimal contact in one specimen of *annulata*. Given these diverging observations and the minute contact that is present in our material, we regard (for now) any contact within the ingroup as an abnormality.

(C) *Absence of the "posterior process of the postorbital" (Hirayama, 1985, 8).*

We cannot determine unambiguously what Hirayama (1985) meant by this character. In our assessment of testudinoids, both a posterolateral and a posteromedial process of the postorbital can occur. In Hirayama's (1985) analysis, only *grandis* and *spinosa* lack a "posterior process of the postorbital." These species are also the only 'batagurid' taxa to fully lack a temporal arch. We suspect that this character may somehow be referring to a lack of a bony temporal arch.

(D) *Processus inferior parietalis "medially approximating each other, cranial cavity anteroventrally narrowing" (Hirayama, 1985, 5; McCord et al., 1995, 7; Yasukawa et al., 2001, 2).*

We acknowledge the validity of this character as was originally worded by McDowell (1964). However, we find it difficult to determine how strongly the constriction of the brain case must be before it can be considered present. We were unable to develop unambiguous discrete character states for this feature.

(E) *Subdivision of the foramen nervi trigemini (Crumly, 1982; Hirayama, 1985, 6).*

This character was used originally by Crumly (1982) to infer phylogenetic relationships within 'Testudinidae'. For his ingroup, Crumly (1982) observed a great amount of polymorphism, with no single species either completely lacking or always exhibiting a subdivision of the foramen. He also noted asymmetry for this character between the left and right side of some individuals. We confirm the common presence of a subdivided trigeminal foramen in representatives of 'Testudinidae,' and the occasional presence in individuals of 'Emydidae' and 'Bataguridae' (e.g., *areolata*, *dentata*, *flavimaculata*, *N. platynota*, and *rubida*). A significant amount of variation can be observed in two specimens of *borneensis* available to us, that exhibit left/right asymmetry and the full spectrum from a fully intact (Fig. 137), to partially subdivided (Fig. 138), to fully subdivided (Fig. 139) trigeminal foramen. Given that most taxa are represented by three or fewer skulls in our study, it is apparent that we are not able to fully document the amount of variation exhibited by testudinoids.

(F) *Contact between postorbital and squamosal (Hirayama, 1985, 9).*

Gaffney et al. (1991) noted that absence of this contact is associated with the upper temporal emargination and considered it informative at the level of their analysis. Within our ingroup, all turtles have substantial upper temporal emarginations, resulting in the contact being just barely present, or just barely absent, or polymorphic (e.g., *picta*, *petersi*, *texana*, *crassicollis*). See comments above under character 9.

(G) *Median premaxillary notch (Hirayama, 1985, 19; Yasukawa et al., 2001, 9)*

(H) *Large cusps near the suture of the premaxillae and maxillae (Hirayama, 1985, 28).*

Initially, we were faced with the problem of defining these two characters independently from one another, because the presence of two tightly spaced, opposing cusp-like structures along any margin will automatically result in the development of a median notch. An additional problem relating to these characters is the question of whether these features should be observed on the ramphotheca or the maxilla.

Large, tooth-like cusps are clearly present in a number of taxa (e.g., *thurjii*) but so is the full spectrum of smaller cusps, making it impossible to clearly define discrete character states. Furthermore, if all species were evaluated for medial notches that existed even if the cusps were removed, all taxa in our sample would show a medial notch. We were unable to develop a consistent method for scoring this character for all testudinoid species.

(I) *"Antero-medial portion of the upper triturating surface formed by premaxillae and maxillae" (Hirayama, 1985, 23; Yasukawa et al., 2001, 13).*

We are neither able to replicate the full meaning of this character nor formulate truly discrete character states. A connection with the development of the secondary palate is evident, but the morphology of this region seems to be sufficiently covered by a number of other characters.

(J) *Participation of the vomer in the foramen praepalatinum (Crumly, 1982, 10; Hirayama, 1985, 32; Yasukawa et al., 2001, 15).*

Within testudinoid turtles, the foramen praepalatinum perforates the nasal cavity at the border between the premaxilla and the vomer. When the foramen is positioned slightly more anteriorly, it is fully surrounded by the premaxilla, when it is minutely farther posterior it is surrounded by the vomer. Considering the impact of such minute changes, it is not surprising that our scoring for this character generally seems to be in conflict with that of Hirayama (1985) and Crumly (1982). This character appears to be subject to great intraspecific variation.

(K) *Foramen palatinum posterius enclosed within the brain cavity (Hirayama, 1985, 34).*

According to Hirayama (1985), in *reevesii* (only) the foramen palatinum posterius is enclosed within the region of the brain cavity due to a flared descending process of the parietal. We cannot confirm this observation for any testudinoid turtles (including three specimens of *reevesii*).

(L) *Participating bones in the processus trochlearis oticum (Hirayama 1985, 37; Gaffney and Meylan, 1988, Gaffney et al. 1991, 6; McCord et al., 1995, 8; Shaffer et al., 1997, 74, 258 Yasukawa et al., 2001, 18).*

The relative participation of the prootic, parietal, and quadrate to the processus trochlearis oticum was used previously by a number of authors to infer phylogenetic relationships within turtles. Our observations confirm the great variety of morphologies that can be observed in this region. However, the amount of intraspecific variation is considerable and the full spectrum of possible morphologies seems to be filled, making it difficult to discern discrete character states. Future research in the area may result in more clearly defined discrete character states.

(M) *Length of the crista supraoccipitalis (Hirayama, 1985, 40).*

A long crista supraoccipitalis was observed by Hirayama (1985) for *borneensis*. The character states he used are defined by relative length of the crista supraoccipitalis to the "condylo-basal length." Unfortunately, we could not replicate this because it is not clear exactly how the length of the crista was measured. Furthermore, a true morphological gap seems to be missing between the admittedly very long crista of *borneensis* and other 'batagurids' with an elongated crista. This character is problematic, because it is poorly defined and lacks discrete character states.

(N) *Bony sutures and sulci lost in old adults (Hirayama, 1985, I).*

According to Hirayama (1985), loss of sutures and sulci occurs in *baska*, *borneoensis*, and *borneensis* only. We are able to confirm this, but we do not have individuals of all other species that are sufficiently old enough to positively confirm that they also do not exhibit this feature at old age. In subsequent treatments, loss of sutures and loss of sulci should be treated as separate characters.

(O) *Ossification of cornu branchiale II (Hirayama, 1985, 48; Yasukawa et al., 2001, 20).*

This character was used previously to unite tortoises with a number of 'batagurid' taxa (Hirayama, 1985). The hyoid apparatus of turtles is often disarticulated in skeletal preparations, making is difficult to positively confirm if an ossified cornu branchiale is present or absent. However, for those taxa for which we were able to observe the hyoid apparatus, we were not able to confirm Hirayama's (1985) observation of a reduced cornu branchiale II in some 'batagurids' (e.g., *galbinifrons*, *spengleri*). Instead, these taxa exhibit a cornu branchiale II that is not significantly different from most other 'batagurids.'

(P) *Double articulation between the fifth and sixth cervical vertebrae (Hirayama, 1985; Gaffney and Meylan, 1988, F1.5).*

Most articular surfaces of the cervical column are rather homogenous within all testudinoid turtles (Williams, 1950). A double articulation between the fifth and sixth cervical previously was considered to be a unique character that unites the 'Emydinae' (McDowell, 1964). This character also was used by Hirayama (1985) and with reservations by Gaffney and Meylan (1988). Our observations generally confirm the presence of a more or less clear double articulation in most 'emydids,' however, this features is also present in a number of 'batagurids' confirming that this character is highly variable within the ingroup (Williams, 1950; Gaffney and Meylan, 1988). Unfortunately, discrete character states are lacking; we were able to observe the full morphological spectrum from a clear singular articulation to a clear double articulation.

(Q) *Scapular prong with lateral concavity (Hirayama, 1985, E).*

Hirayama (1985) reported this character as an autapomorphy for *subtrijuga* only. However, we cannot identify this morphology in any of our specimens of *subtrijuga*.

(R) *Large facet of the ilium for the testoscapularis and testoiliacus (Hirayama, 1985, T; Yasukawa et al., 2001, 34)*

(S) *Extensive development of both testoscapularis and testoiliacus (Hirayama, 1985, U).*

An extensive development of the testoscapularis and testoiliacus muscles together with an associated large scar on the ilium was reported by Bramble (1974) for Asian and North American box turtles. Whereas we have no reason to doubt his assessment of the development of these muscles for box turtles, we were not able to score this character for most of the remaining taxa. The shape of the ilium was explored and illustrated for some 'emydids' and 'batagurids' by Yasukawa et al. (2001:122-123).

(T) *Ossification of the epipubis (Gaffney and Meylan, 1988, F5.5).*

The identification (and confirmation of presence or absence) of an ossified epipubis (Fig. 141) is somewhat difficult for most species, because it seems to ossify rather late in ontogeny, and can fall off during preparation. Our tentative observations confirm the presence of an ossified epipubis in numerous adult 'emydids' and 'batagurids,' typically terrestrial forms (e.g., *T. ornata*, *G. insculpta*, *N. platynota*, *yuwonoi*). An improved sample of adult specimens of all taxa, however, is necessary to reveal the true distribution of this character.

(U) *Diploid Number of Chromosomes (Hirayama, 1985, Ø; Shaffer et al., 1997, 43).*

The diploid number of chromosomes was used by Carr and Bickham (1986) to hypothesize a sister group relationship between the 'Emydinae' and *subtrijuga*, followed by *borneensis* and *crassicollis* and finally the rest of the 'Batagurinae.' Whereas most 'batagurids' allegedly have 52 chromosomes, *subtrijuga*, *borneensis*, *crassicollis*, and 'emydids' are supposed to have 50 chromosomes. We view these results with caution, because a brief review of the relevant literature reveals great differences in chromosomal counts for a variety of taxa. For instance, according to the work of Killebrew (1977) and Bickham (1981), *amboinensis* has 52 chromosomes, however, Gorman (1973) reported only 50. Similar conflicts can also be found for *dentata* (Bickham, 1981; DeSmet, 1978; Gorman, 1973; Stock, 1972), *subtrijuga* (Bickham, 1981; Killebrew, 1977), *trijuga* (DeSmet, 1978; Carr and Bickham, 1986), *sinensis* (Bickham, 1981; Killebrew, 1977; Stock, 1972), *crassicollis* (Killebrew, 1977; Stock, 1972; Bickham and Baker, 1976), and some of the species currently placed in *Graptemys* (Killebrew, 1977; McKown 1972), *Trachemys* (DeSmet, 1978; Killebrew, 1977; Stock, 1972) and *Mauremys* (Killebrew, 1977; Stock, 1972). This conflict in primary data is probably best understood when considering the nature of testudinoid chromosomes: whereas 14 pairs of chromosomes have a considerable size, all of the remaining ones are extremely small. Given these circumstances, it seems reasonable to hypothesize that one pair of chromosomes may be unrecognized during analysis.

(V) *Plica media spade-shaped (Gaffney and Meylan, 1988, F7.1).*

The penile soft anatomy of turtles was comprehensively reviewed by Zug (1966) and one of his characters, the shape of the plica media, was used by Gaffney and Meylan (1988) to unify species placed in *Chrysemys*, *Deirochelys*, *Trachemys*, and *Pseudemys* as a monophyletic group. In his detailed description of the plica media, Zug (1966) referred to the shape of this structure as being "spade-shaped" in those taxa, but made similar claims for other taxa too. Furthermore, based on the illustrations that were provided by Zug (1966) for other taxa, the plica media of species placed in *Graptemys*, *Malaclemys*, *Rhinoclemmys*, and *Platysternon* appear "spade-shaped" also, even though Zug (1966) did not explicitly use those descriptive words. This anatomical system should be carefully reevaluated for all testudinoids, with special attention given to definition of discrete characters.

(W) *Ossifications within the fenestra postotica.*

In some taxa, portions of the fenestra postotica are closed or obscured by ossifications (noted, but without exemplars, by Gaffney, 1972). In our largest specimen of *grandis* (CAS 228443) a short, spike-like ossified process extends posterodorsally from the dorsal edge of the quadrate process of the pterygoid, and crosses the fenestra postotica. It is situated ventral to the stapes (columella auris), medial to the incisura columella auris, and lateral to the fenestra ovalis (Fig. 141). In some specimens, the dorsal tip of a similar structure approaches or meets a posterodorsally-inclined process that extends from the dorsal surface of the pterygoid, near the suture with the prootic. In our largest specimen of *N. platynota* (CAS 228342) the two processes meet to enclose the stapedial shaft in a ring of bone situated at approximately the midpoint between the fenestra ovalis and the medial opening of the incisura columella auris. Our other, smaller, specimen of *N. platynota* shows no development of these processes. It seems likely that there is an ontogenetic component in the expression of this feature. It does not appear to have any systematic significance, but in any case it is not widespread within Testudinoidea.

Conclusions

Our observations can be used to draw some tentative conclusions regarding the current level of understanding about morphological variation within testudinoid turtles. In addition, we provide some cautionary statements about the quality of morphological data now in use for assessing systematic relationships among these turtles. It is clear from a perusal of the relevant literature, and from our data, that there is reasonably strong morphological support for a monophyletic 'Testudinidae.' Support for monophyly of 'emydines' and 'batagurines' is not as impressive. The paraphyly of 'Batagurinae' (with respect to 'Testudinidae') was explicitly proposed by Hirayama (1985) and has been generally accepted since that time, although some strides have been made towards resolving relationships among some 'batagurine' taxa. The monophyly of 'Emydinae' seems to have been implicitly assumed by many workers, but remains to be established in the context of a rigorous phylogenetic analysis of all relevant taxa. The interpretation of several morphological features shared between some 'emydines' and some 'batagurines' as either convergence or synapomorphy remains an important and interesting challenge. For example, there are intriguing morphological similarities between *subtrijuga* and some species classified in the genus *Graptemys* (e.g., contact of the jugal and descending process of the parietal; contact of the quadratojugal with the articular facet of the quadrate; contact between the quadratojugal and the maxilla; ventral process of the pterygoid approaching the articular surface of the quadrate). These similarities may be due to functional convergence as a result of a molluscivorous diet, but they raise questions about the propriety of utilizing *subtrijuga* as an outgroup for systematic studies of 'emydines' (e.g., Burke et al., 1996). Additional similarities are reported for chromosome numbers in *subtrijuga* and 'emydines' (see 'Problematic Character' U, above).

A seriously deficient understanding of morphological variation is one of the greatest inadequacies of current perspectives on morphological data in turtles generally, and testudinoids specifically. Few published studies have been conducted to evaluate the range and causes of sexual, ontogenetic, intra- and inter-population variation in morphological characters within testudinoids. Our preliminary considerations of ontogenetic variation, combined with reports of sexual variation (e.g., Berry and Shine 1980; Gibbons and Lovich, 1990; Stephens, 1998) and new studies exploring the complex interactions of morphological evolution with behavioral characteristics and environmental conditions in turtles (e.g., Lindeman, 2000; Herrel et al., 2002; Joyce and Gauthier, 2003; Claude et al., 2003) emphasize the importance of pursuing these questions further. Our decision not to produce a phylogenetic hypothesis in this paper was based primarily on two considerations. The first is the relatively small sample size we used for many taxa in this study (although it is comparable to sample sizes from other, previously published, studies), and the fact that several taxa are not represented in our work. The second consideration is our sense that the current understanding of morphological variation in testudinoid turtles is insufficiently mature to permit reliable phylogenetic hypotheses based solely on morphological data. The most expedient way to address the need for greater documentation of variation within testudinoid species is to utilize existing museum collections to the greatest extent possible, and secondarily to develop responsible collecting programs that are designed with this need in mind.

Our results also indicate that morphological data matrices currently in the literature should not be taken at face value. We had particular difficulties replicating some of the scoring in the Hirayama (1985) matrix. That seminal analysis (completed prior to the widespread use of computer-assisted analytical methods in systematics) laid the foundation for nearly all subsequent work on 'batagurine' morphology (including our own), and its importance in shaping our current conceptualization of 'batagurine' phylogeny cannot be overstated. The work of pathfinders in all fields of inquiry is often subjected to the greatest scrutiny by the next generation of researchers. Our statements and contradictory observations in this paper in no way denigrate Hirayama's work; instead, we view our efforts as minor attempts to correct the few inconsistencies in his analysis, and to contribute our observations to the body of knowledge that he began to synthesize 20 years ago.

The accurate interpretation and understanding of the morphological descriptions of previous authors were among the great challenges we faced when we began our studies of testudinoid skeletal morphology. Much of our confusion could have been averted if adequate illustrations accompanied all published character descriptions, but such documentation often is an expensive undertaking. Our photographs of character states discussed in this paper are intended to facilitate communication among turtle enthusiasts, and to provide a baseline for future comparisons and discussions about testudinoid morphology. We hope that adequate illustration of all newly proposed characters will become standard practice among turtle systematists. It seems likely that our interpretations of characters will differ in some respects from those of our colleagues, and we anticipate that our decisions regarding 'problematic characters' (discussed above), and our choices with respect to 'lumping' or 'splitting' previously published character states, will generate much spirited discussion in the years ahead.

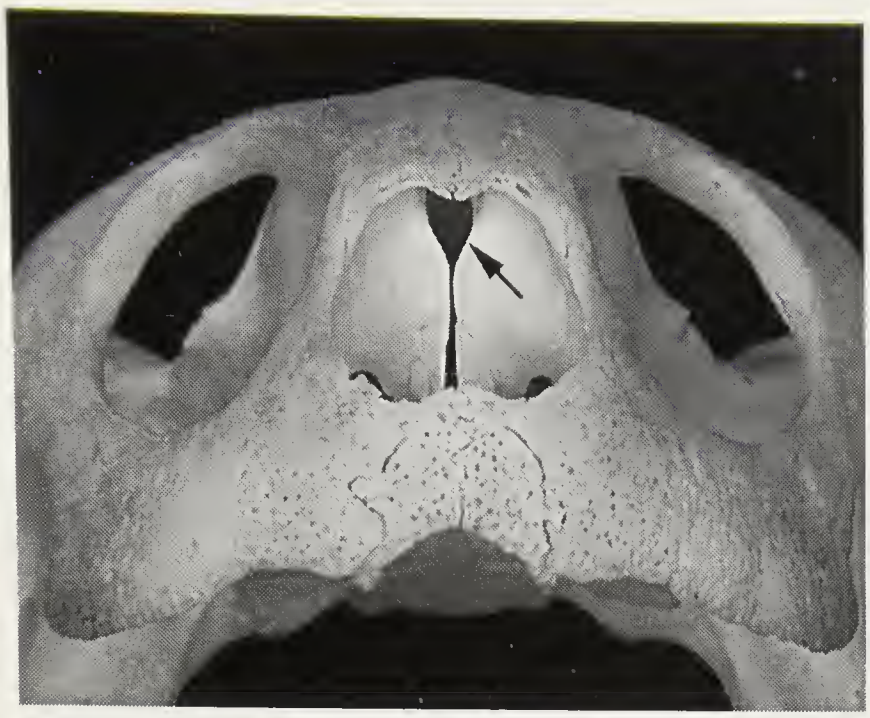

Figure 1. Character 1(0): CAS 228437, *texana*, anterior view.

Figure 2. Character 1(1): CAS 228404, *belliana*, anterior view.

Figure 3. Character 2(0): CAS 228458, *texana*, left lateral view.

Figure 4. Character 2(1): CAS 228404, *belliana*, left lateral view.

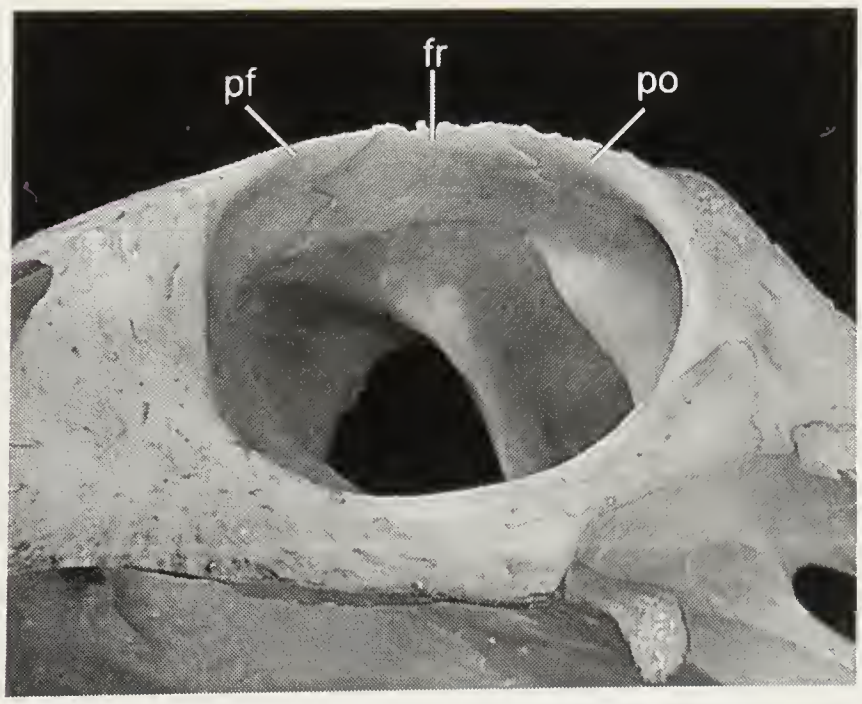

Figure 5. Character 3(0): CAS 228444, *mouhotii*, left ventrolateral view of orbit.

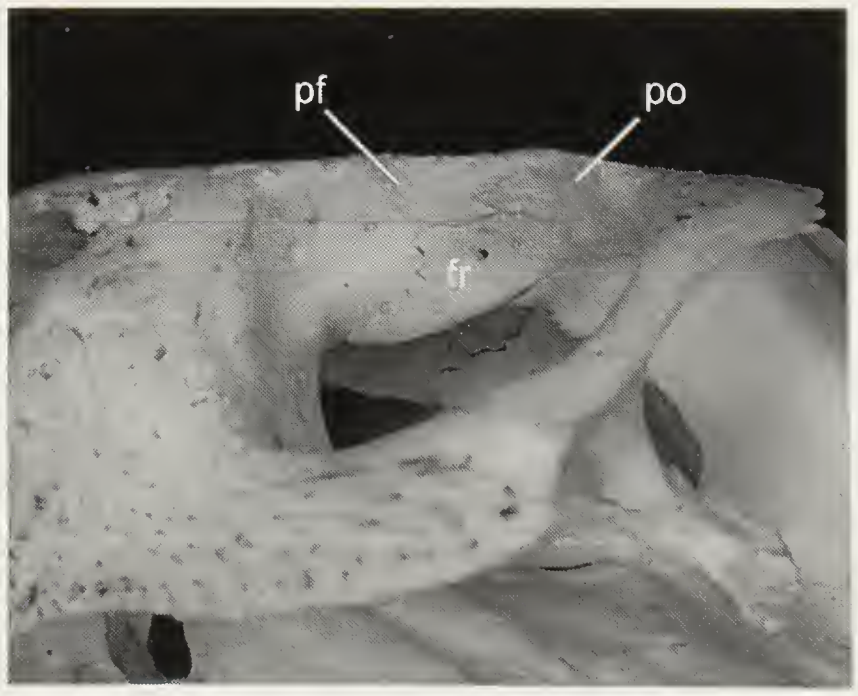

Figure 6. Character 3(1): CAS 228443, *grandis*, left ventrolateral view of orbit.

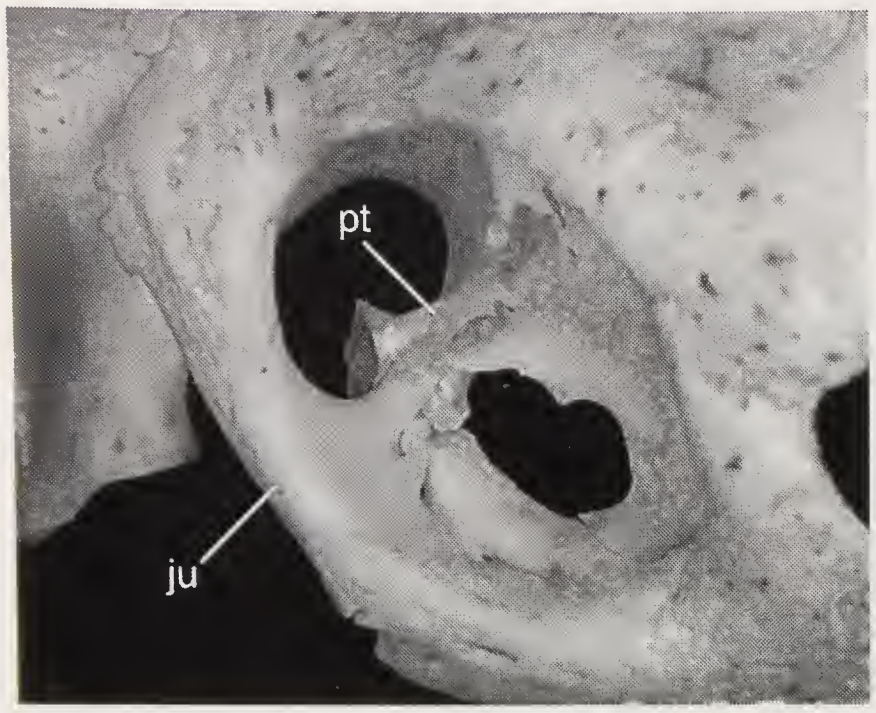

Figure 7. Character 4(0): CAS 228443, *grandis*, right anterolateral view of orbit.

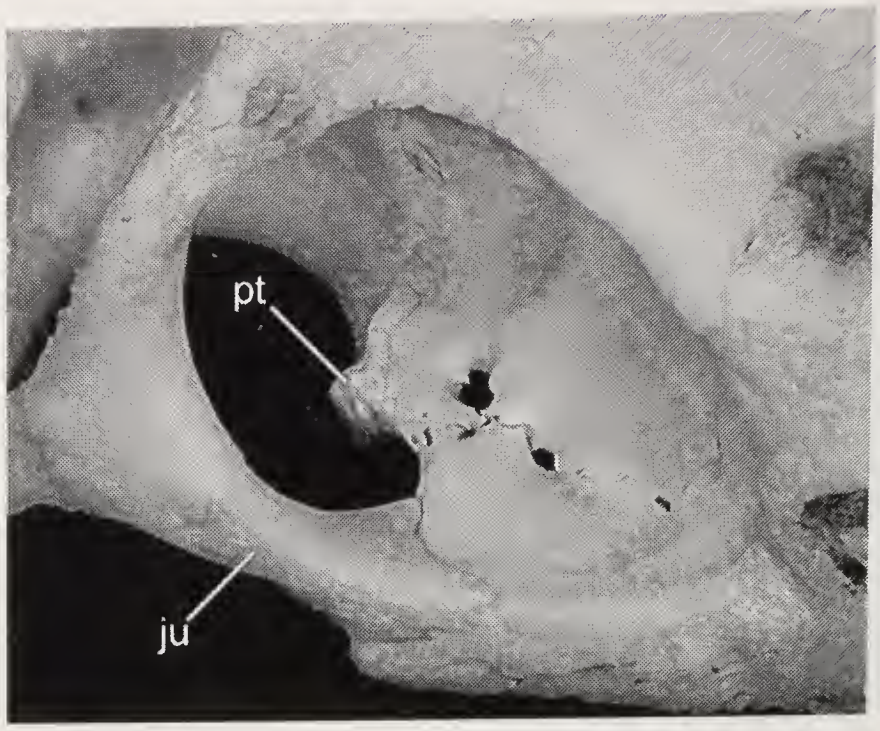

Figure 8. Character 4(1): CAS 228420, *mouhotii*, right anterolateral view of orbit.

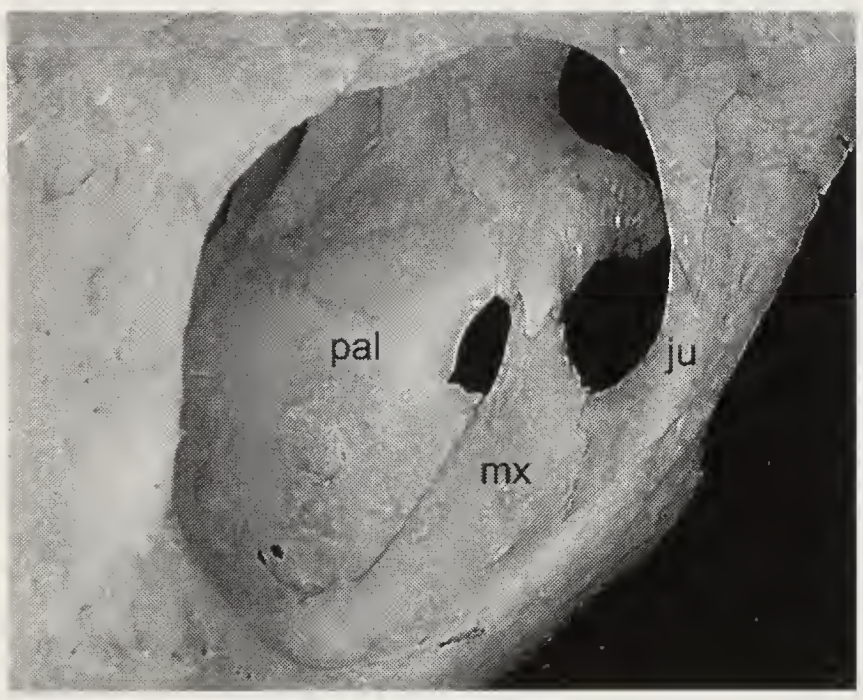

Figure 9. Character 5(0): CAS 228444, *mouhotii*, left anterolateral view of orbit.

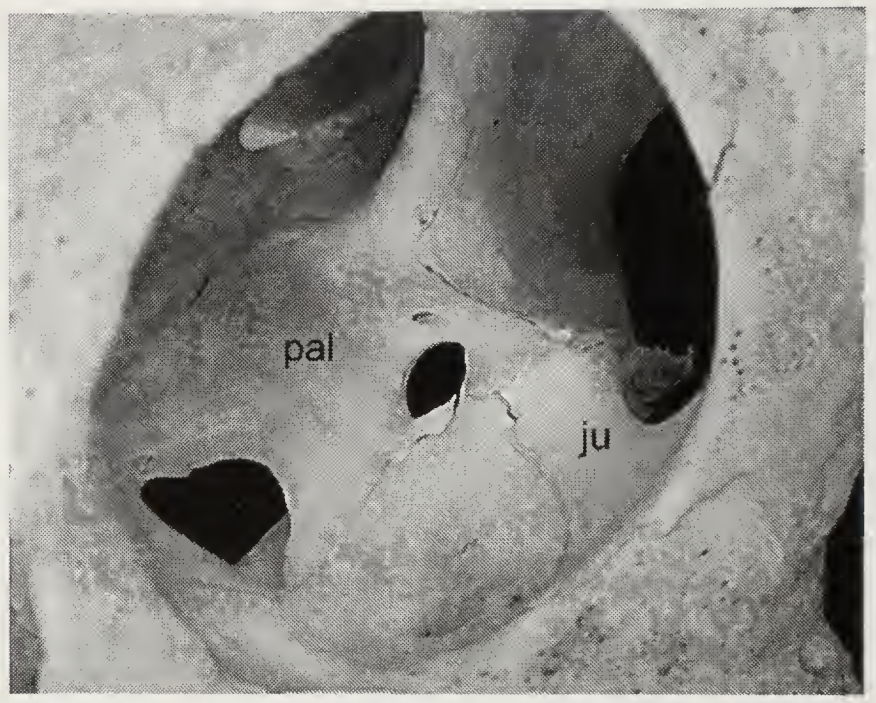

Figure 10. Character 5(1): CAS 228438, *texana*, left anterolateral view of orbit.

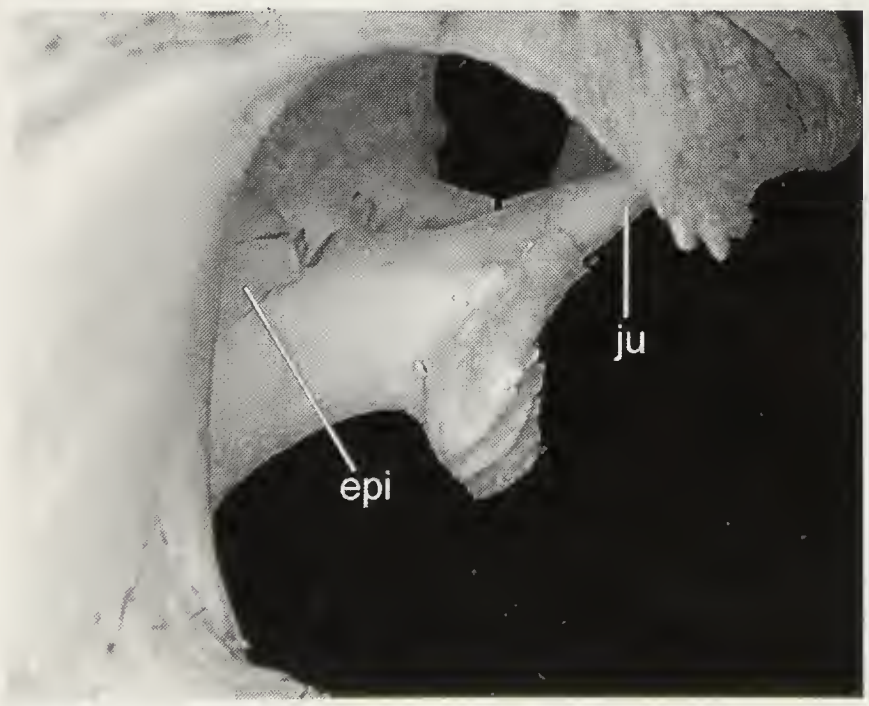

Figure 11. Character 6(0): CAS 228443, *grandis*, right posterolateral view.

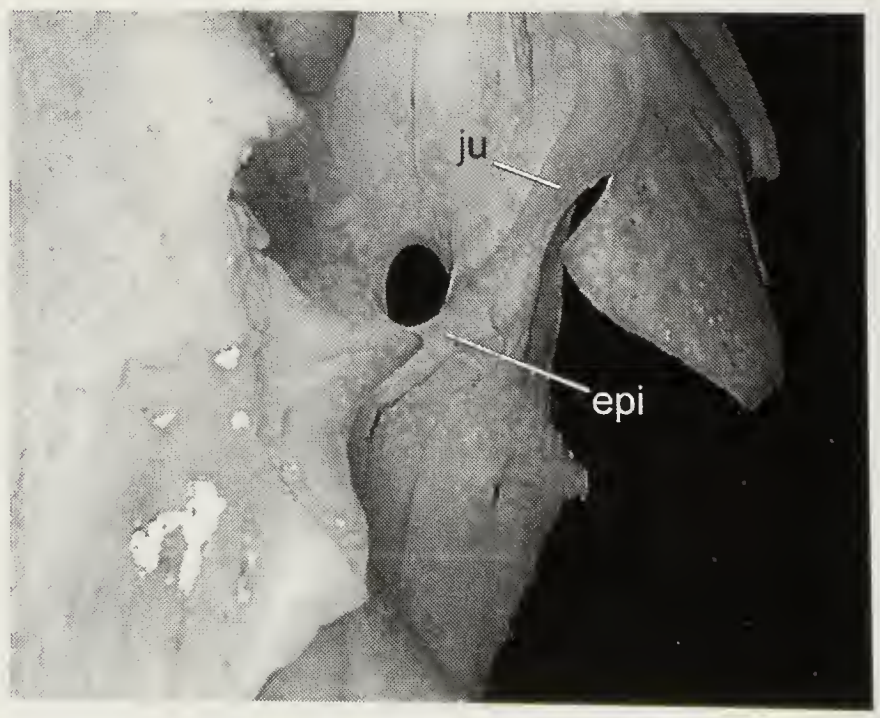

Figure 12. Character 6(1): CAS 228439, *texana*, right posterolateral view, postorbital removed.

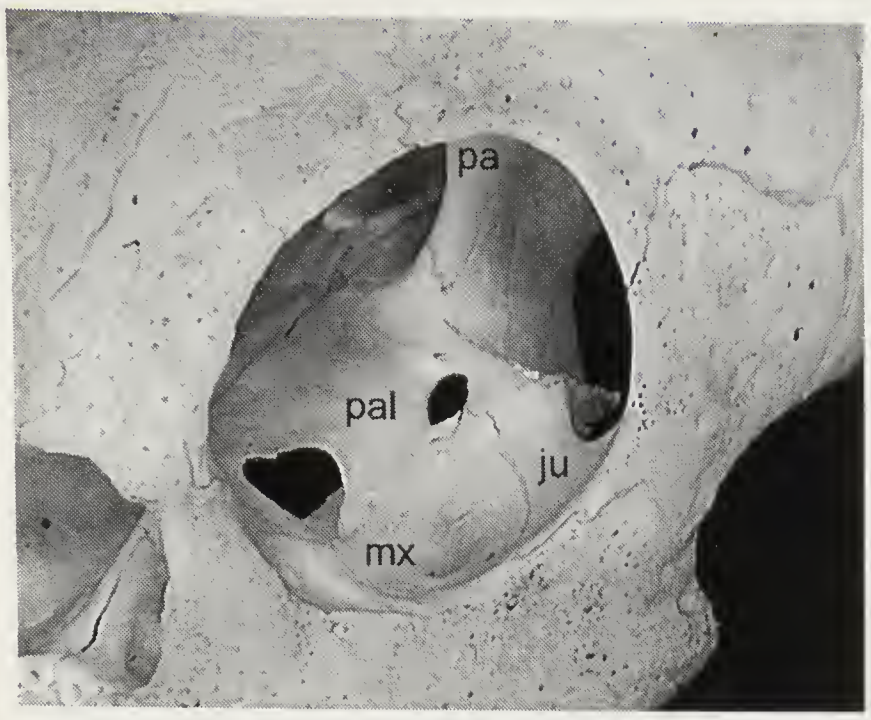

Figure 13. Character 7(0) and 8(0): CAS 228438, *texana*, left anterolateral view of orbit.

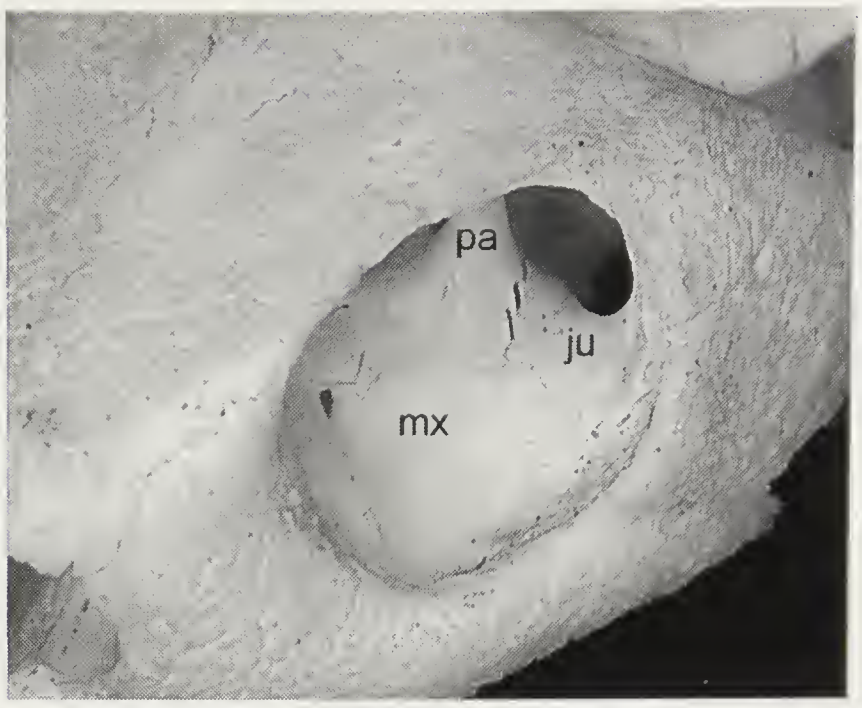

Figure 14. Character 7(1) and 8(1): CAS 228445, *subtrijuga*, left anterolateral view of orbit.

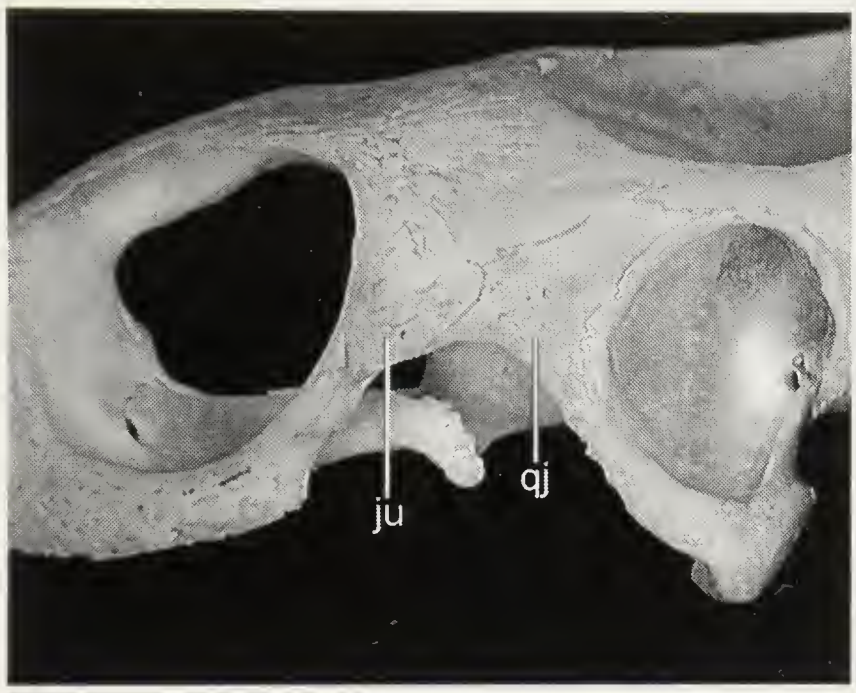

Figure 15. Character 9(0): CAS 228447, *orbicularis*, left lateral view.

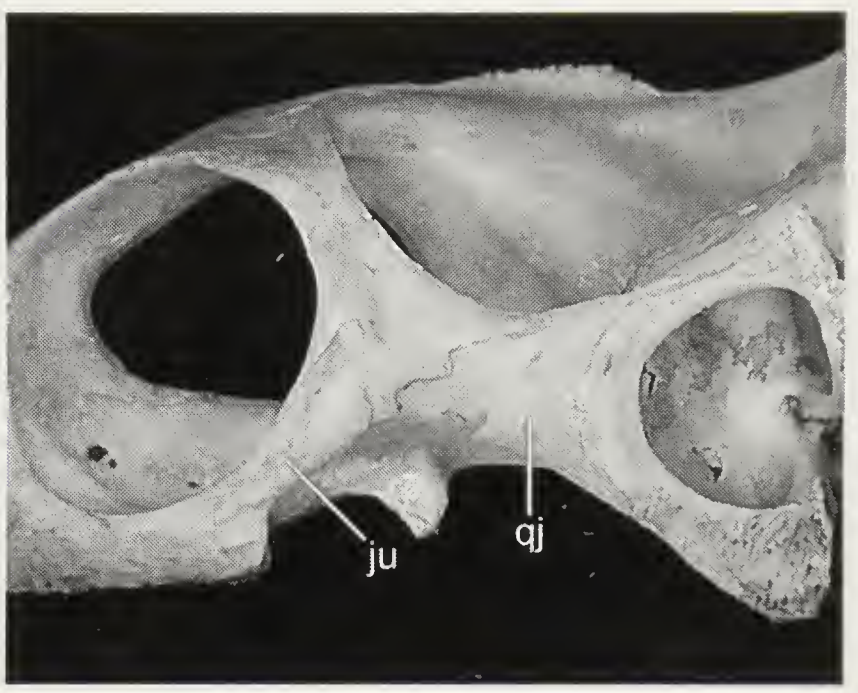

Figure 16. Character 9(1): CAS 228444, *mouhotii*, left lateral view.

Figure 17. Character 9(2): YPM 14074, *galbinifrons*, left lateral view.

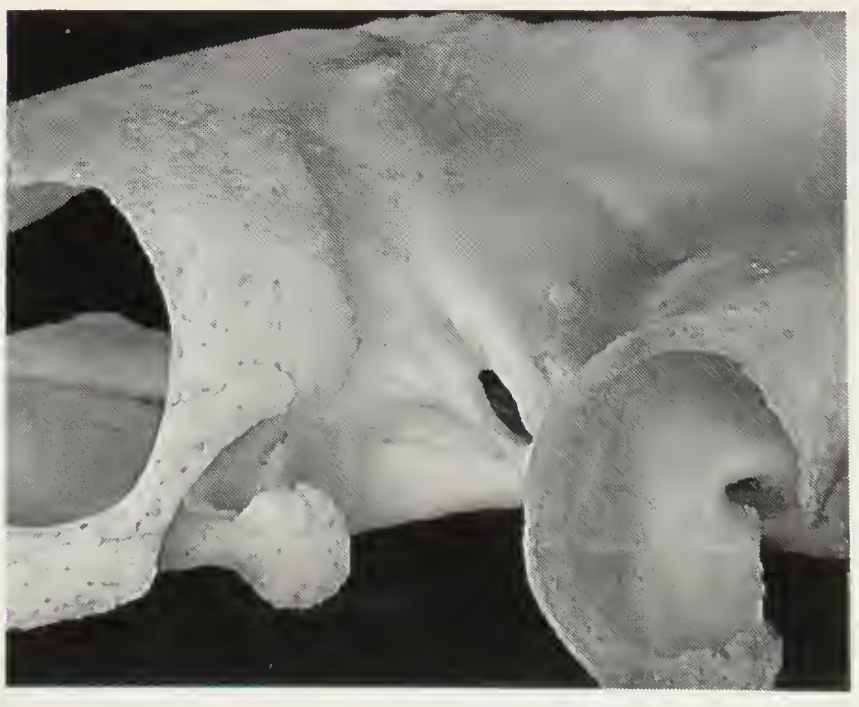

Figure 18. Character 9(2): YPM 14080, *galbinifrons*, left lateral view.

Figure 19. Character 10(0): CAS 228444, *mouhotii*, left lateral view.

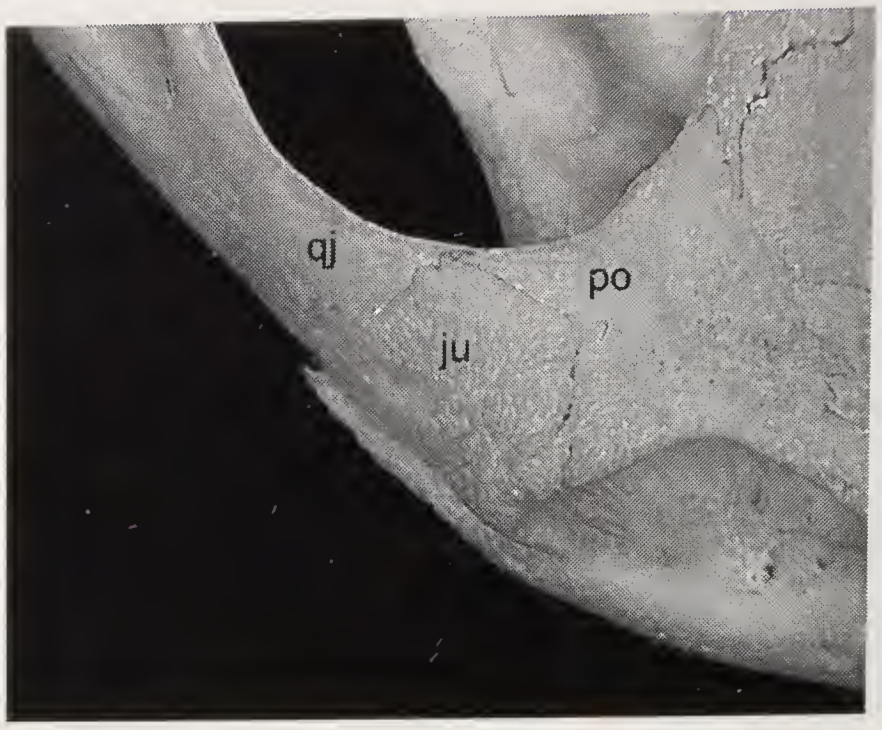

Figure 20. Character 10(0): CAS 228446, *subtrijuga*, left lateral view.

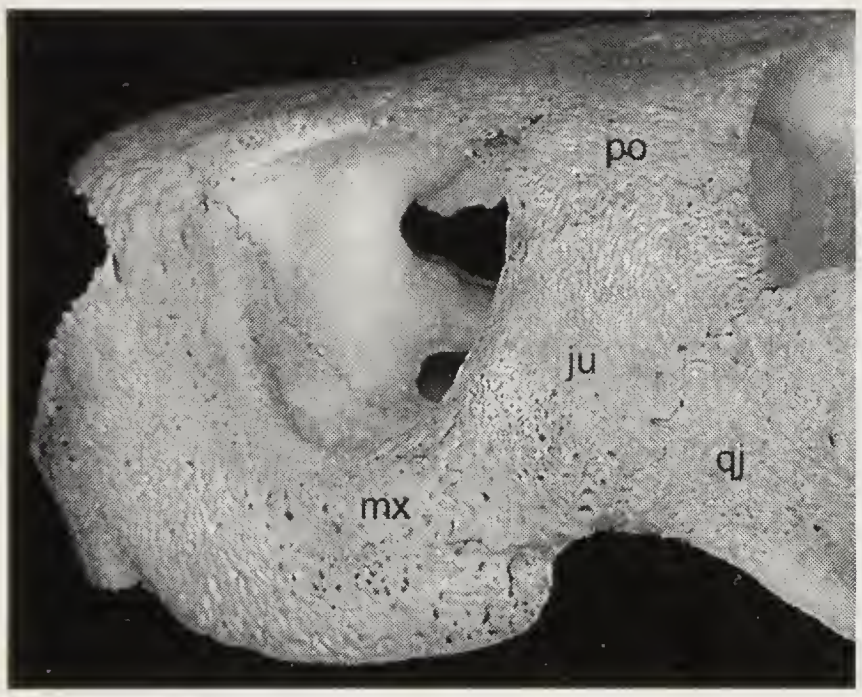

Figure 21. Character 10(1): YPM 10339, *hamiltonii*, left lateral view of orbit.

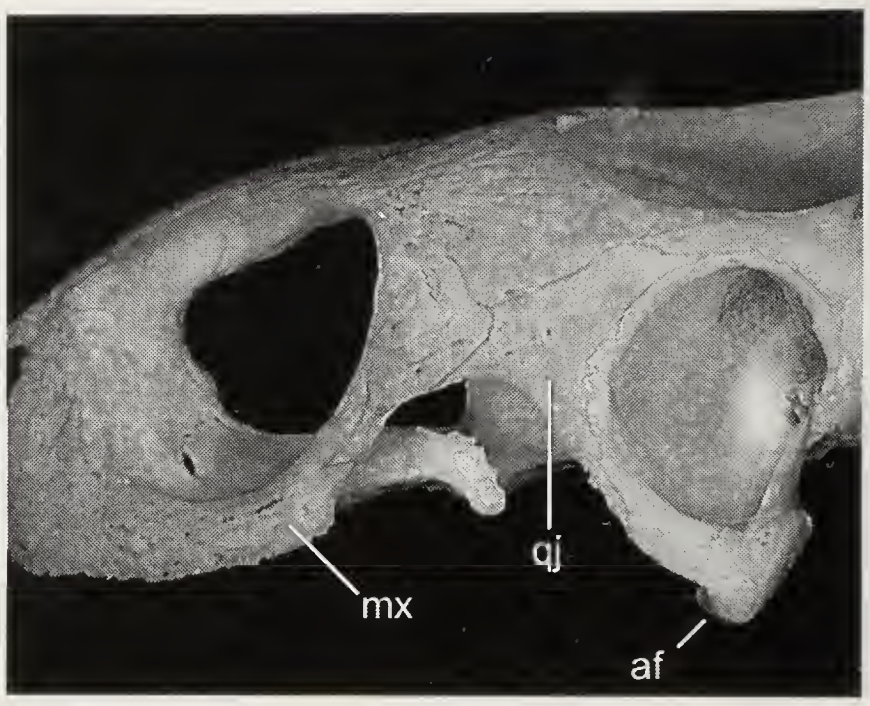

Figure 22. Character 11(0) and 12(0): CAS 228447, *orbicularis*, left lateral view.

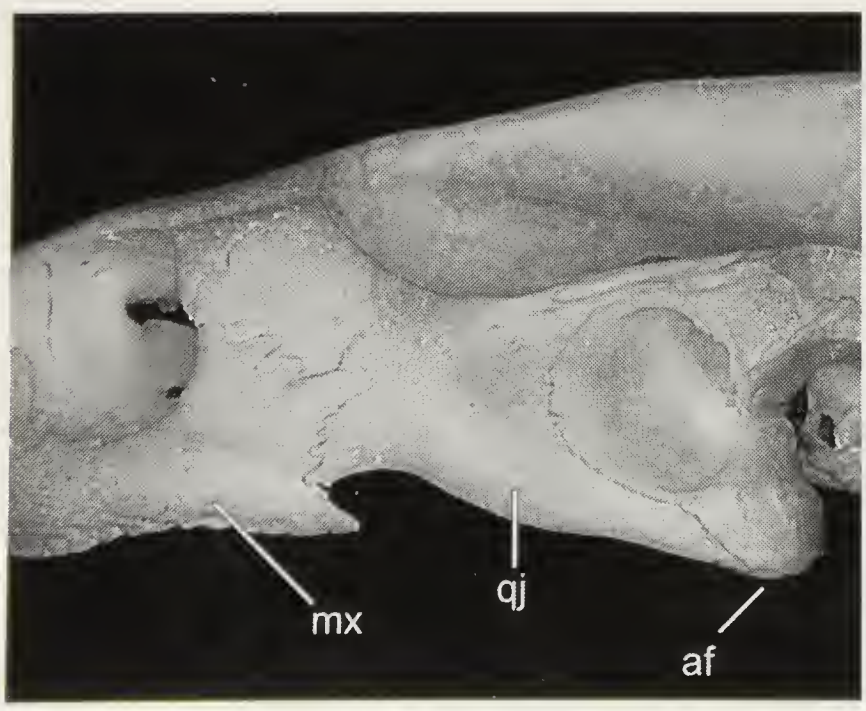

Figure 23. Character 11(1) and 12(1): CAS 228446, *subtrijuga*, left lateral view.

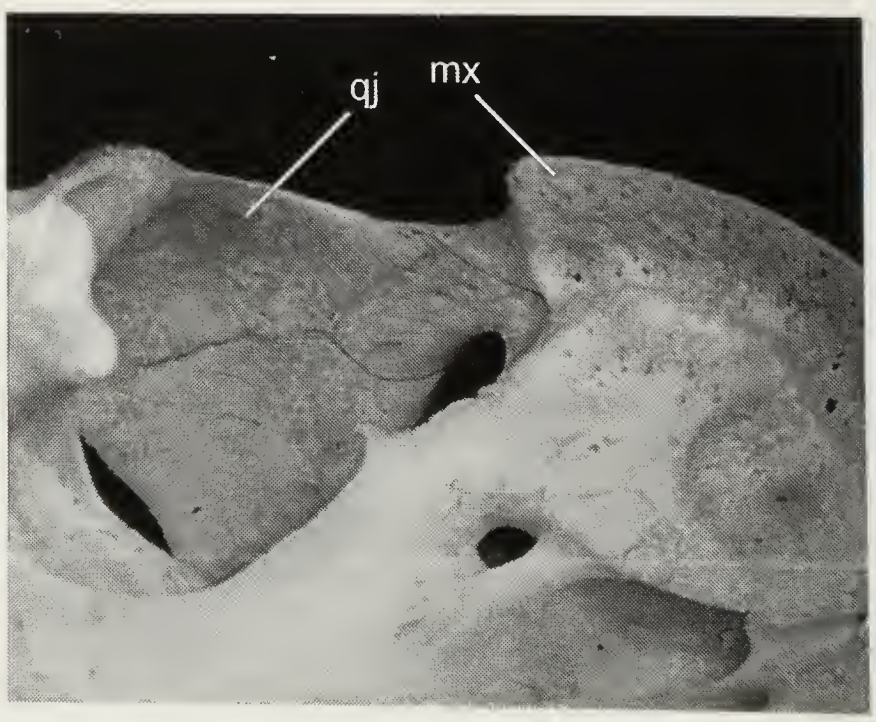

Figure 24. Character 12(1): CAS 228438, *texana*, right posteroventral view of lower temporal fossa.

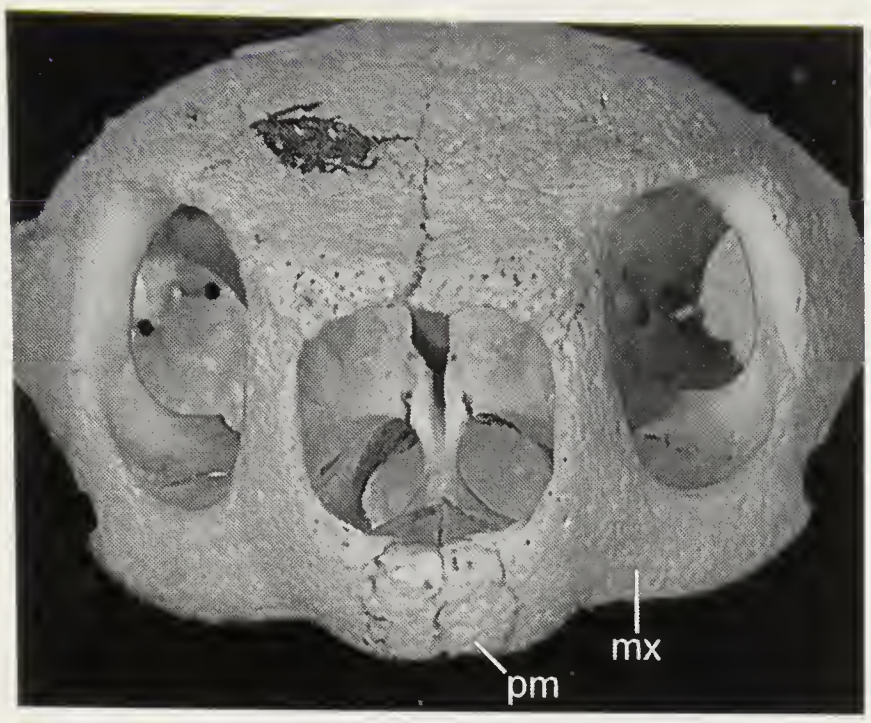

Figure 25. Character 13(0): CAS 228361, *reevesii*, anterior view.

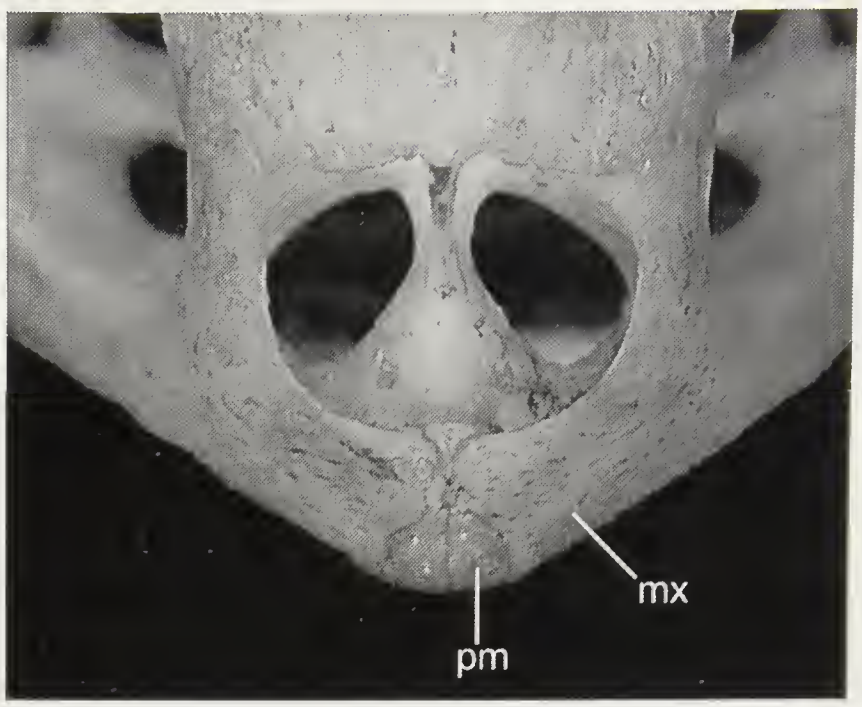

Figure 26. Character 13(0): CAS 228419, *amboinensis*, anterior view.

Figure 27. Character 13(1): CAS 228371, *spengleri*, anterior view.

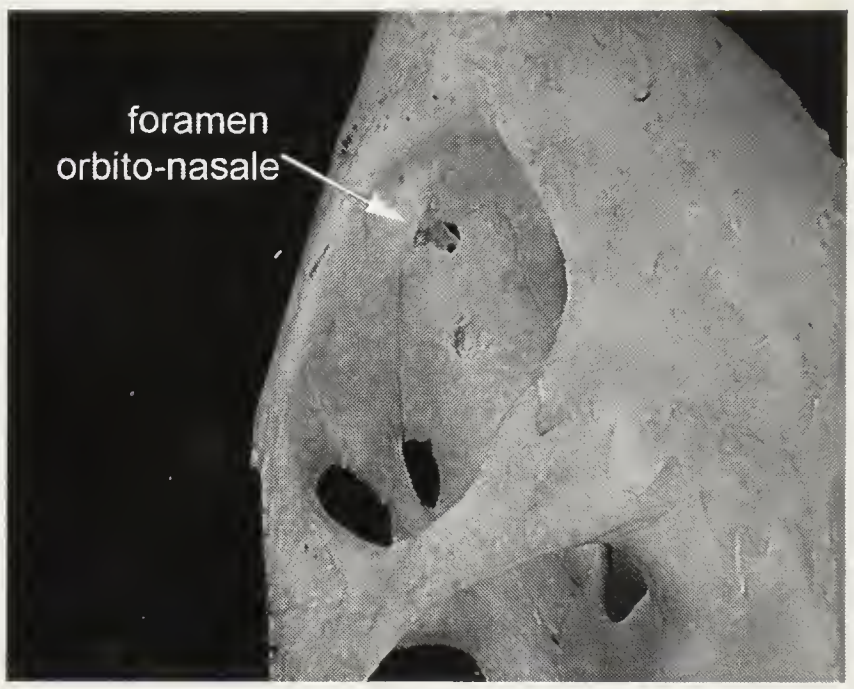

Figure 28. Character 14(0): CAS 228444, *mouhotii*, left posterolateral view of orbit.

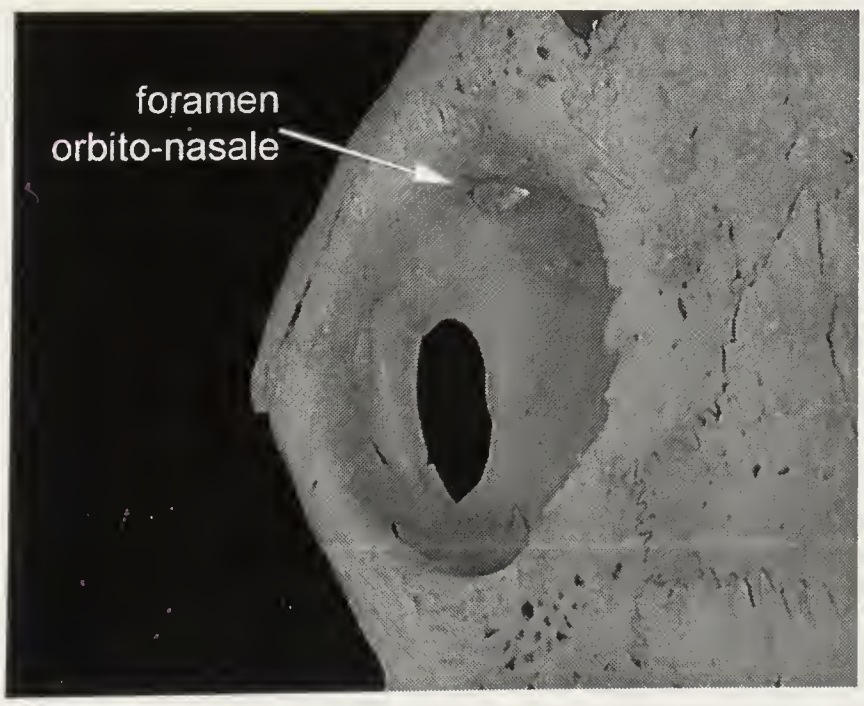

Figure 29. Character 14(0): CAS 228443, *grandis*, left posterolateral view of orbit.

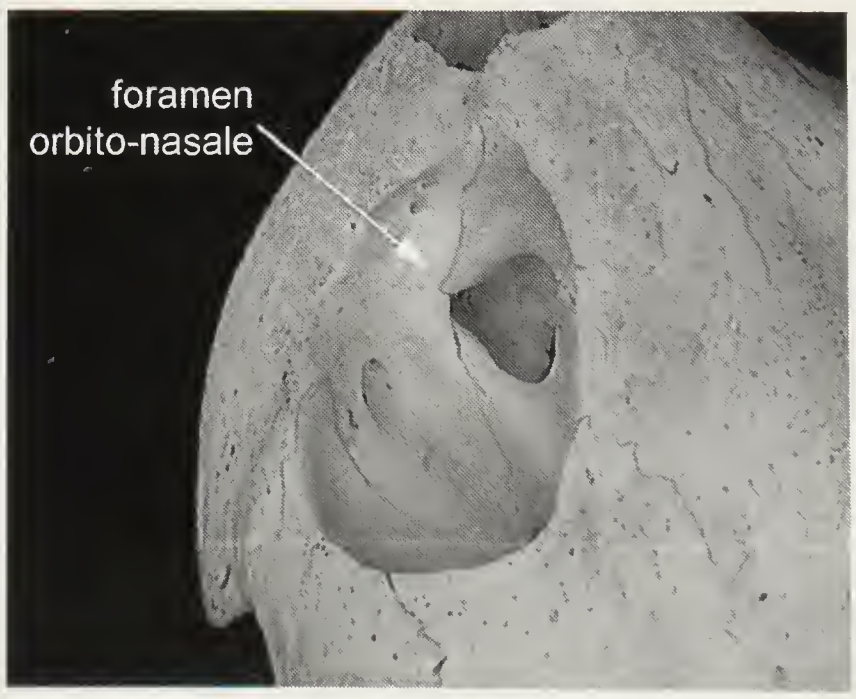

Figure 30. Character 14(1): CAS 228438, *texana*, left posterolateral view of orbit.

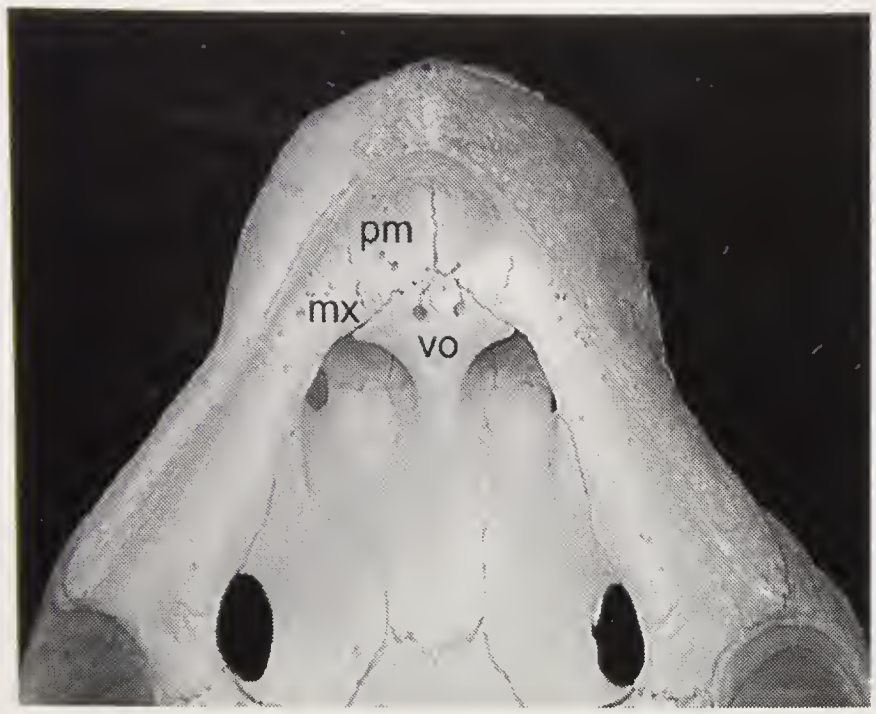

Figure 31. Character 15(0): CAS 228342, *N. platynota*, ventral view of palate.

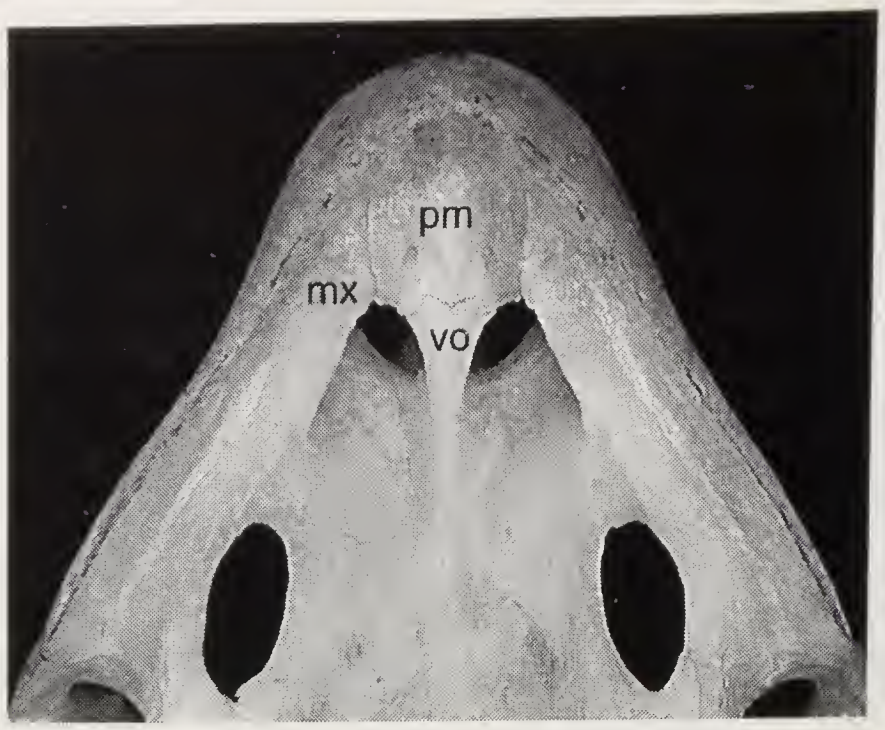

Figure 32. Character 15(1): CAS 228419, *amboinensis*, ventral view of palate.

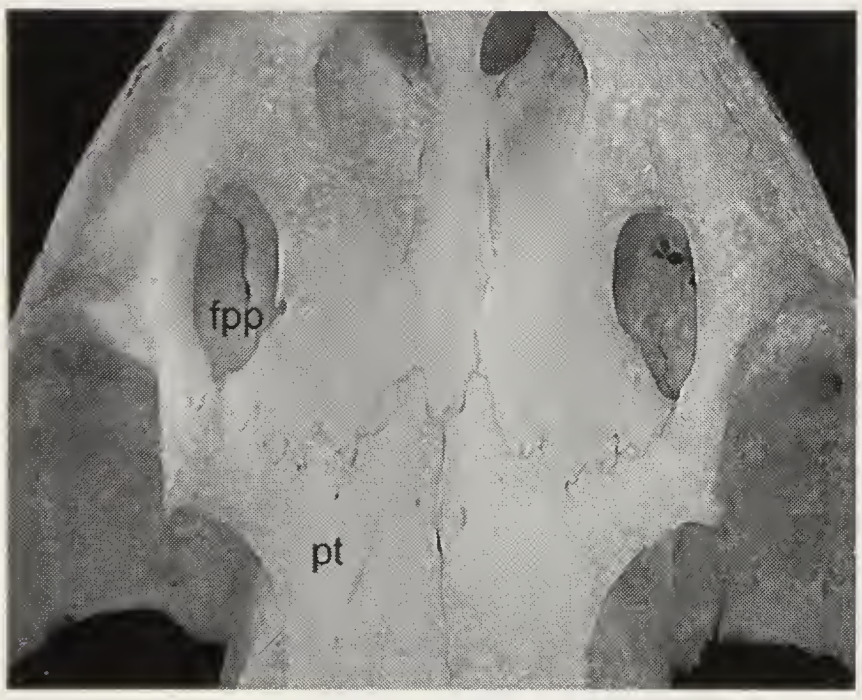

Figure 33. Character 16(0) and 17(0): CAS 228447, *orbicularis*, ventral view of palate.

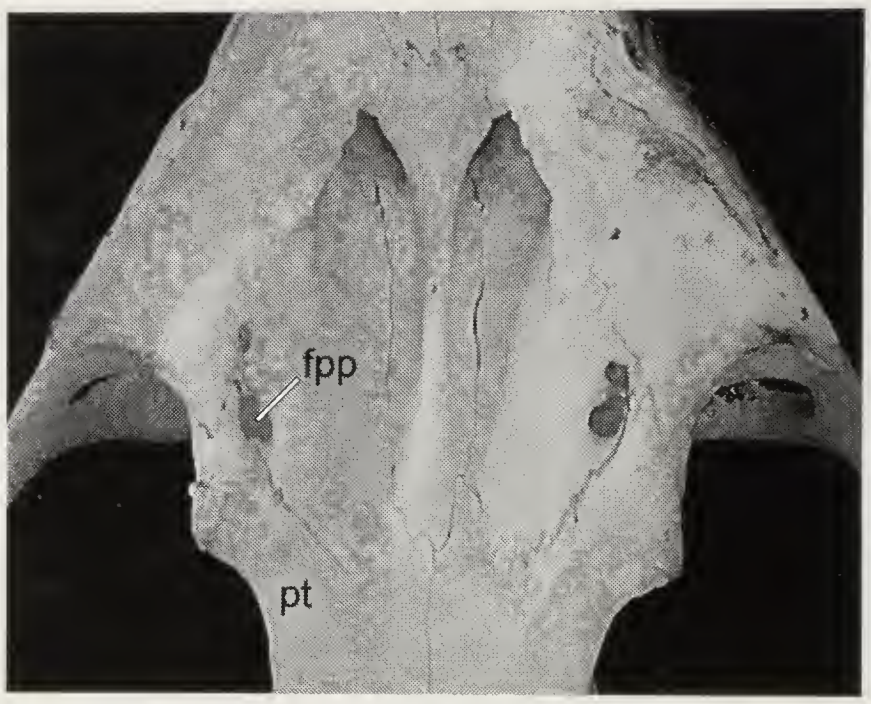

Figure 34. Character 16(1) and 17(1): CAS 228420, *mouhotii*, ventral view of palate.

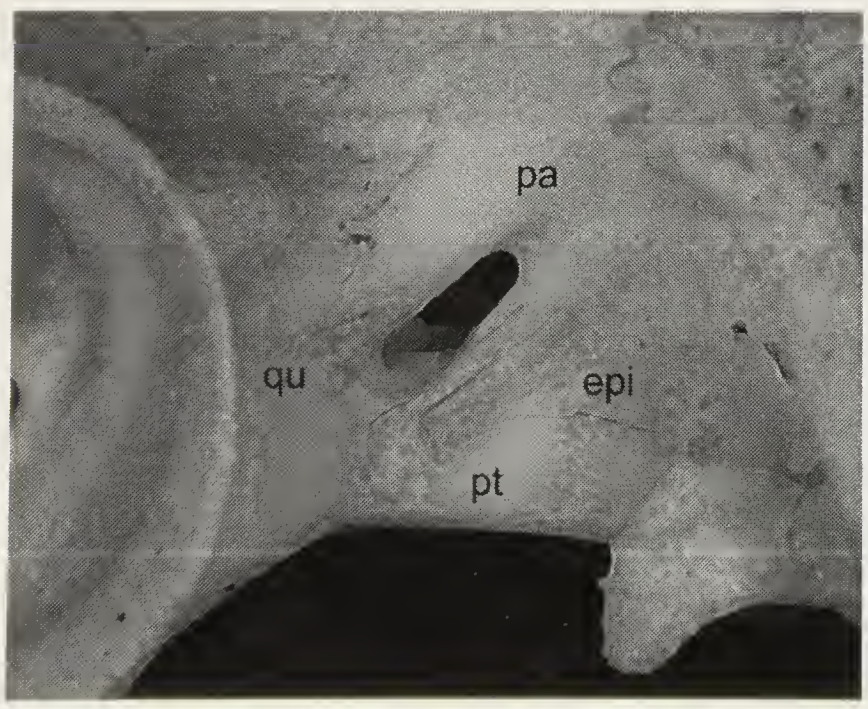

Figure 35. Character 18(0): CAS 228443, *grandis*, right lateral view of trigeminal foramen.

Figure 36. Character 18(1): CAS 228444, *mouhotii*, right dorsolateral view of trigeminal foramen.

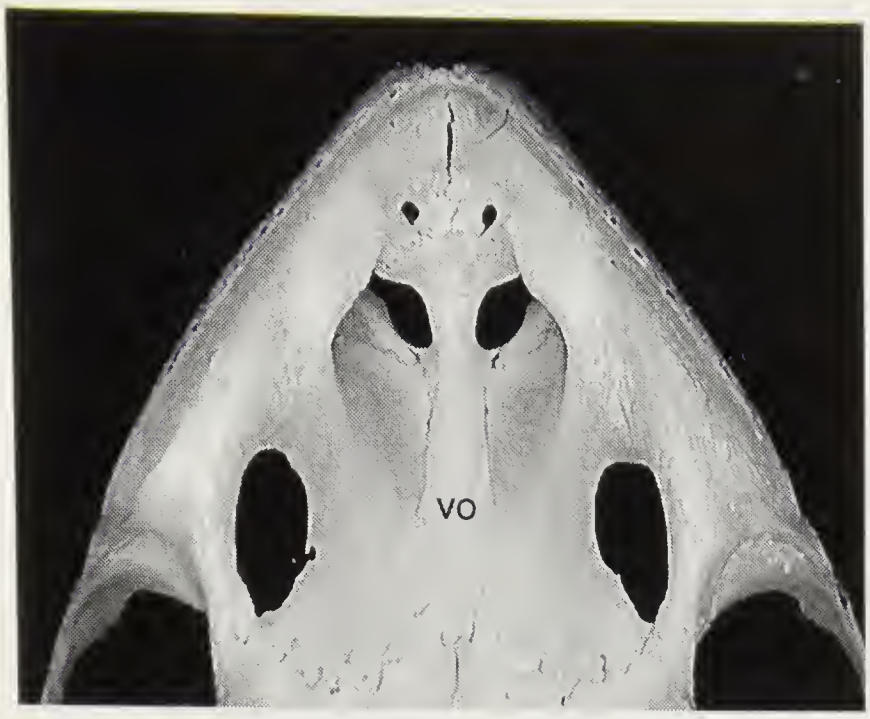

Figure 37. Character 19(0): CAS 228447, *orbicularis*, ventral view of palate.

Figure 38. Character 19(1): TMM 2813, *berlandieri*, ventral view of palate.

Figure 39. Character 20(0): CAS 228335, *crassicollis*, ventral view of palate.

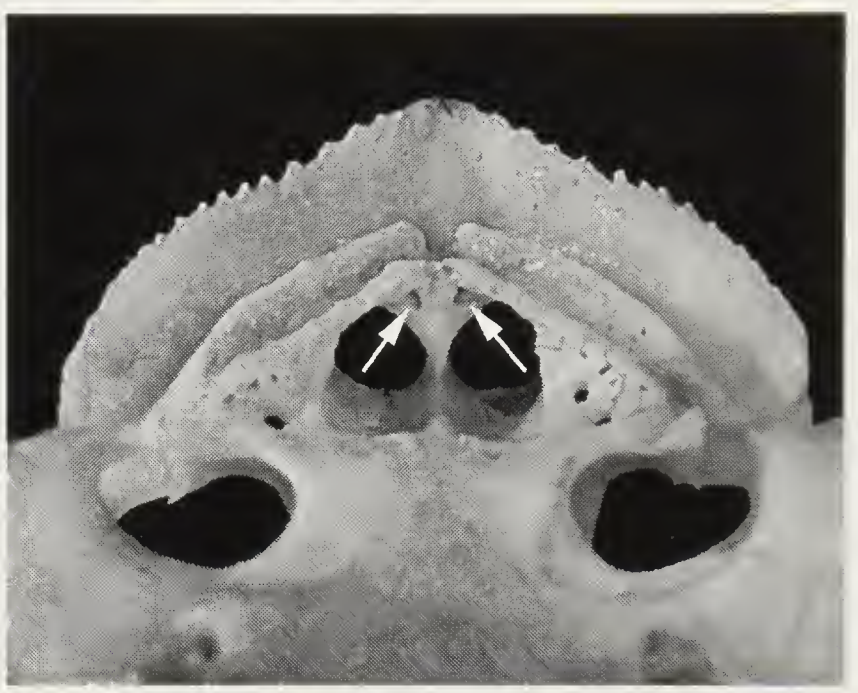

Figure 40. Character 20(1): FMNH 259430, *tentoria*, posteroventral view of palate.

Figure 41. Character 21(0): CAS 228443, *grandis*, ventral view of brain case.

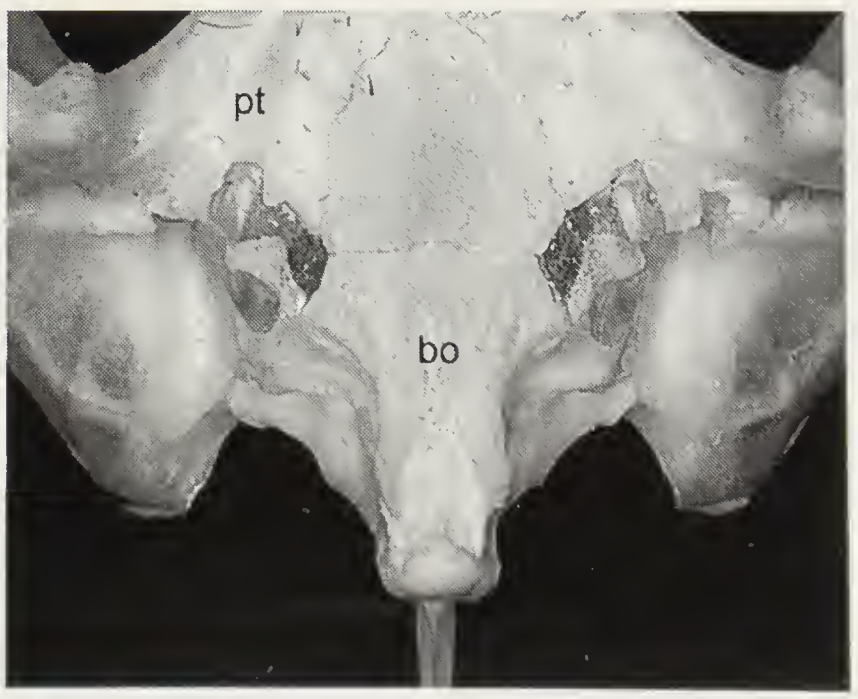

Figure 42. Character 21(1): CAS 228338, *reticularia*, ventral view of brain case.

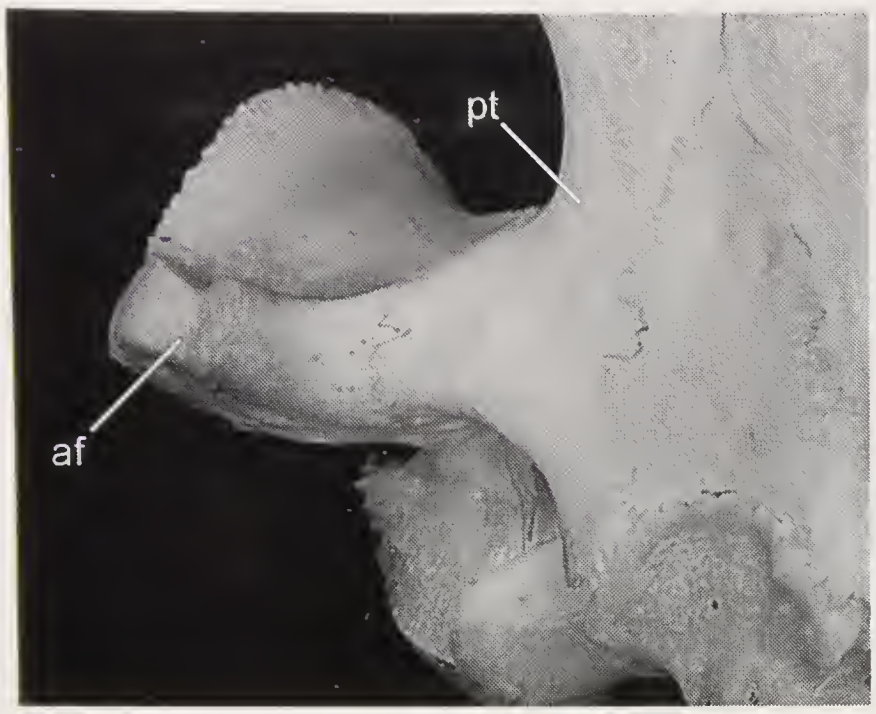

Figure 43. Character 22(0): CAS 228443, *grandis*, ventromedial view of right basicranium.

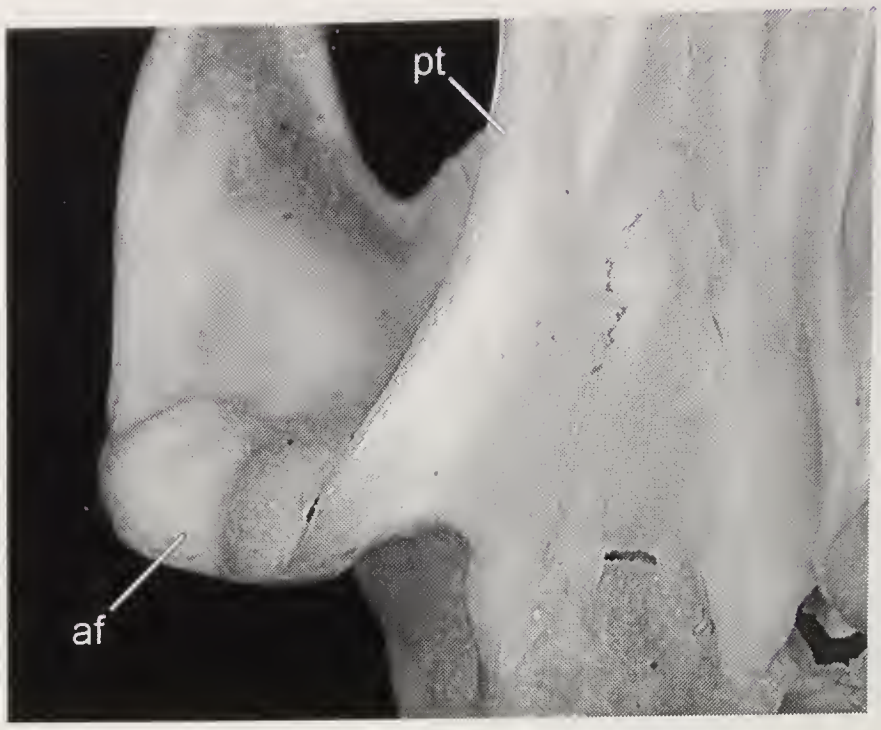

Figure 44. Character 22(1): CAS 228445, *subtrijuga*, ventromedial view of right basicranium.

Figure 45. Character 23(0): CAS 228437, *texana*, right lateral view of quadrate.

Figure 46. Character 23(1): CAS 228342, *N. platynota*, right lateral view of quadrate.

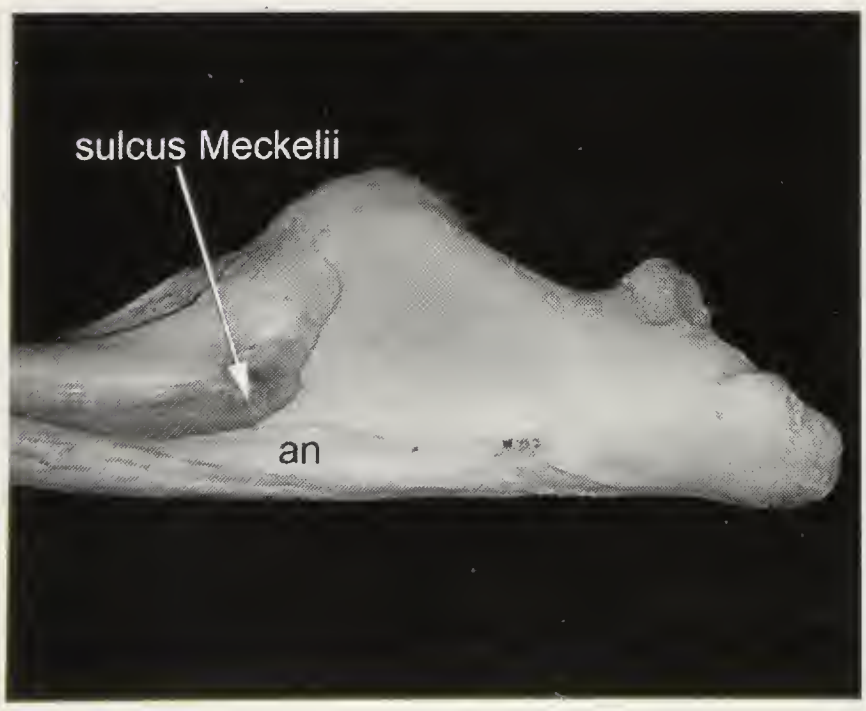

Figure 47. Character 24(0): CAS 228447, *orbicularis*, right lateral view of mandible.

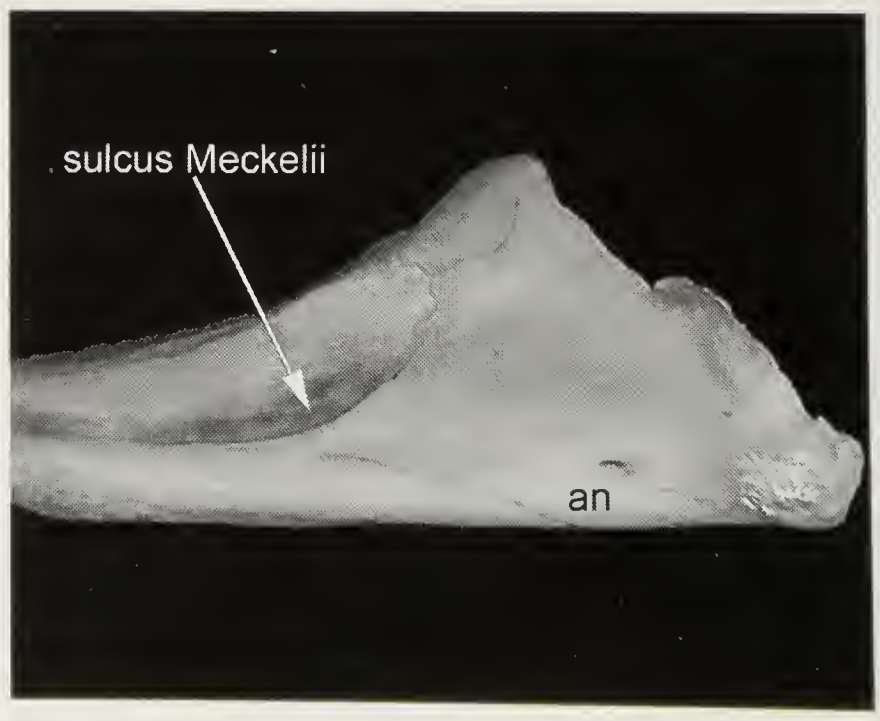

Figure 48. Character 24(1): CAS 228335, *crassicollis*, right lateral view of mandible.

Figure 49. Character 25(0): CAS 228447, *orbicularis*, left lateral view of mandible.

Figure 50. Character 25(1): CAS 228411, *carbonaria*, left lateral view of mandible.

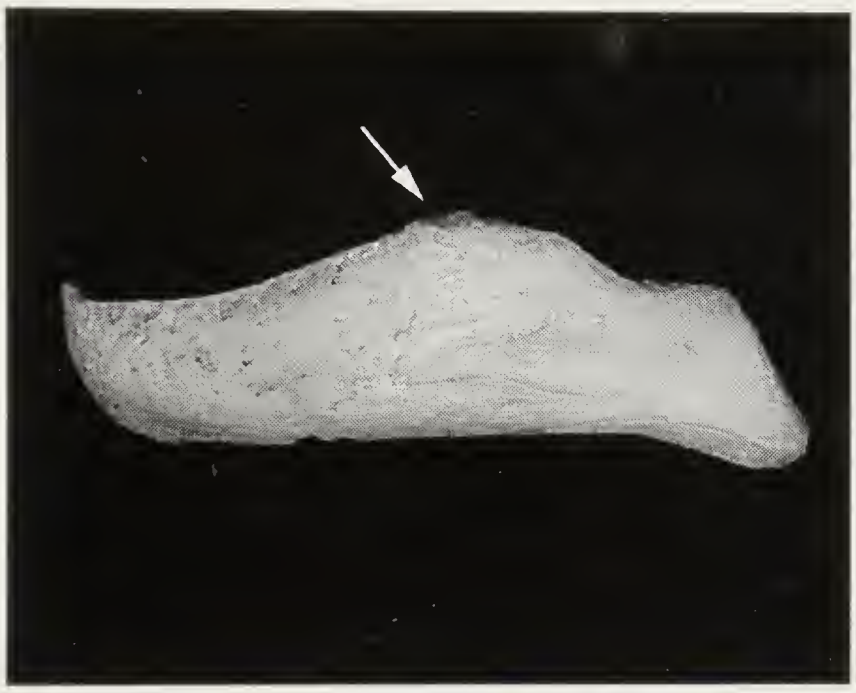

Figure 51. Character 26(0): CAS 228404, *belliana*, left lateral view of mandible.

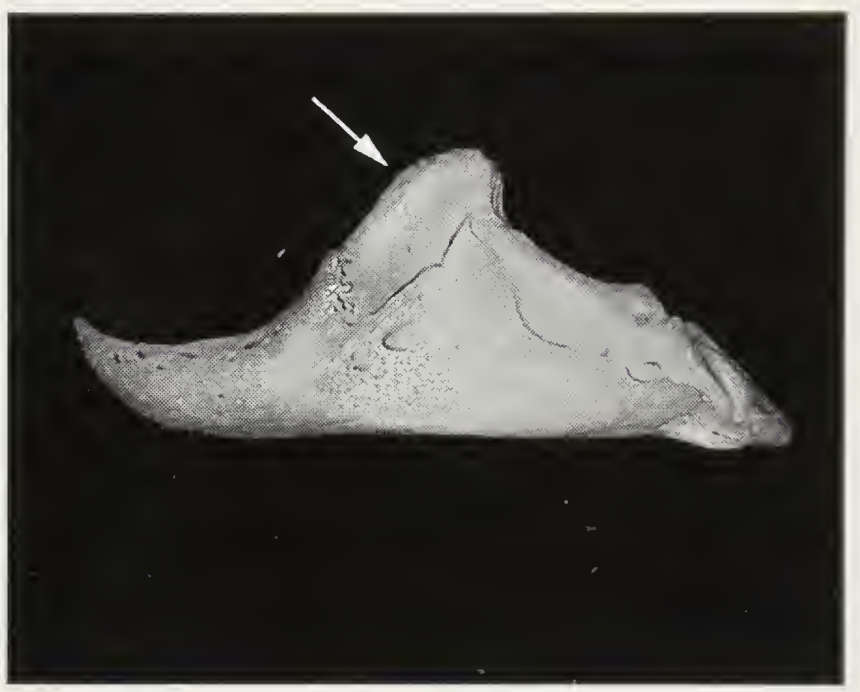

Figure 52. Character 26(1): CAS 228361, *reevesii*, left lateral view of mandible.

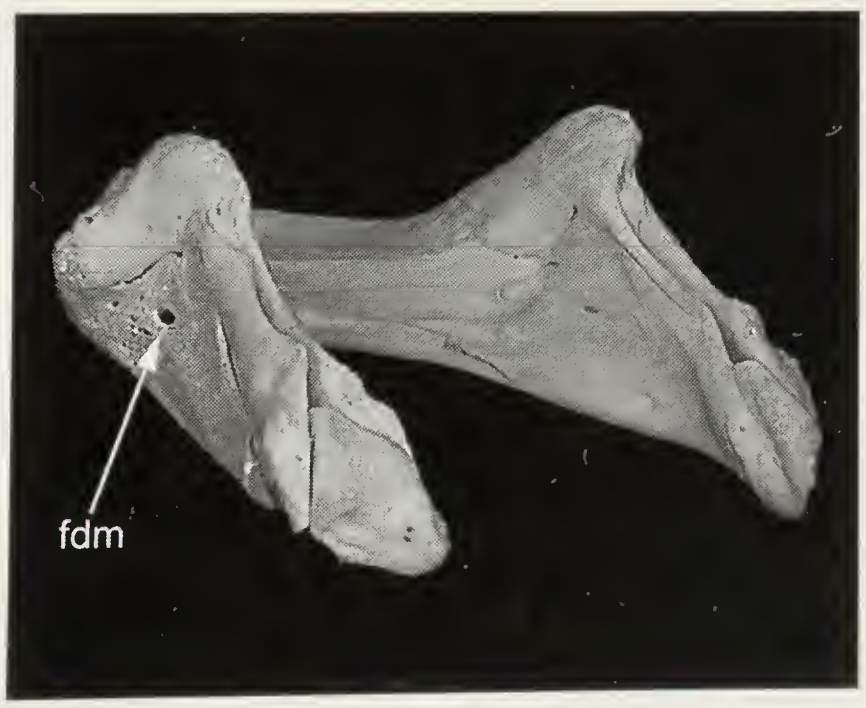

Figure 53. Character 27(0): CAS 228361, *reevesii*, left posterolateral view of mandible.

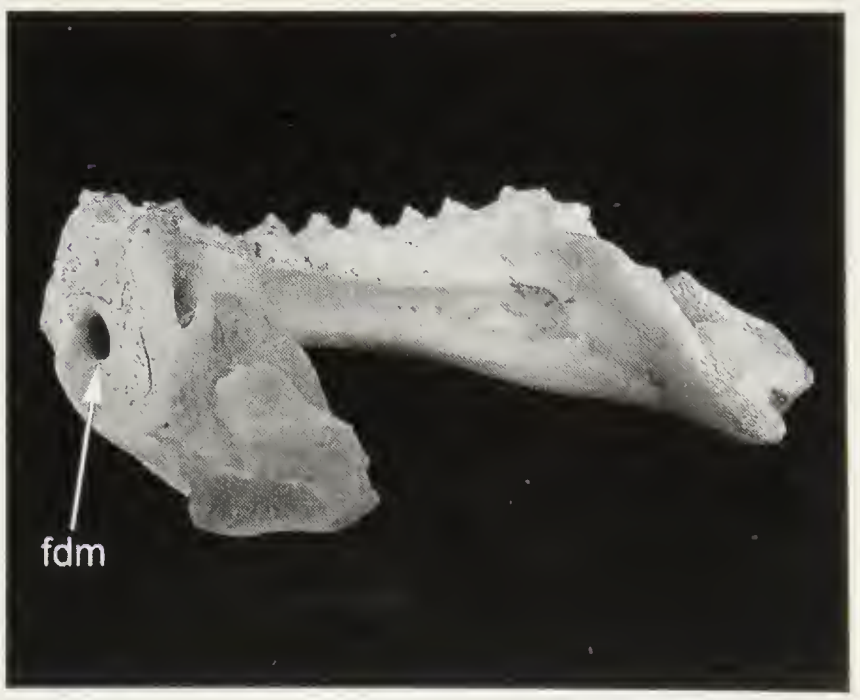

Figure 54. Character 27(1): YPM 10861, *thurjii*, left posterolateral view of mandible.

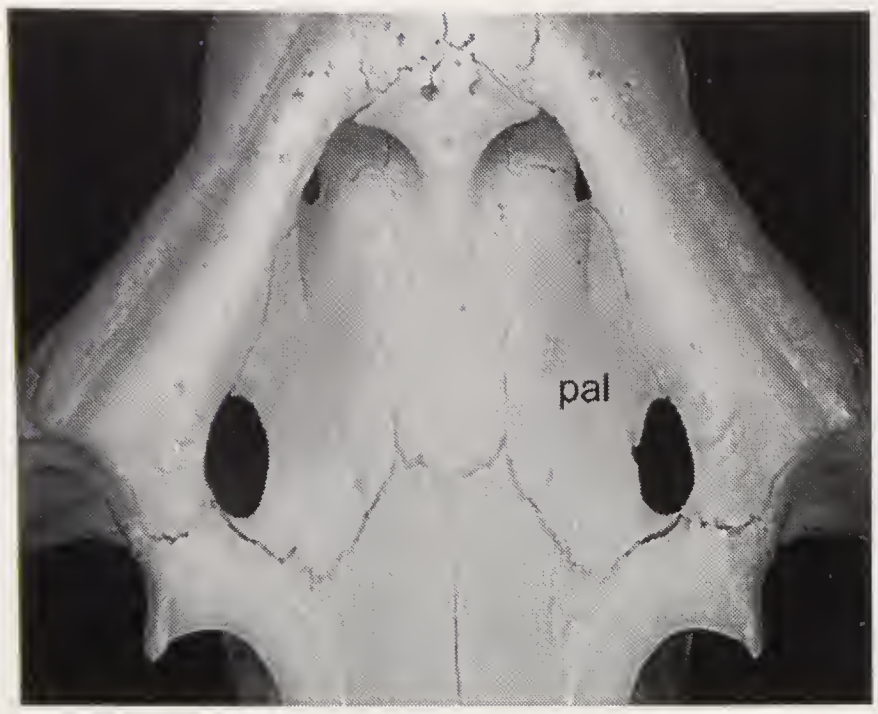

Figure 55. Character 28(0): CAS 228342, *N. platynota*, ventral view of palate.

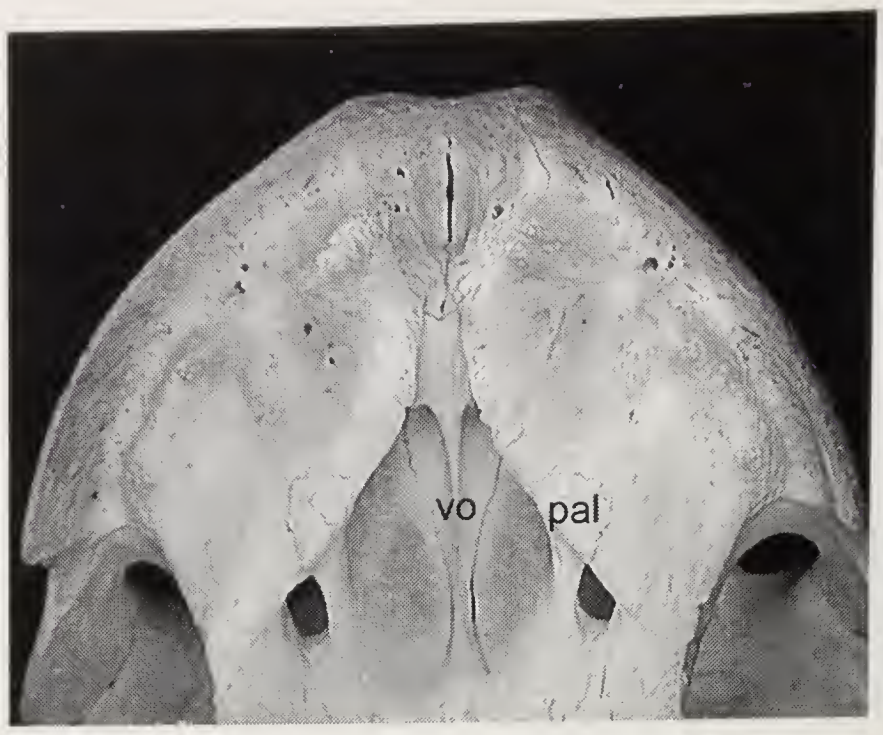

Figure 56. Character 28(1) and 29(0): CAS 228437, *texana*, ventral view of palate.

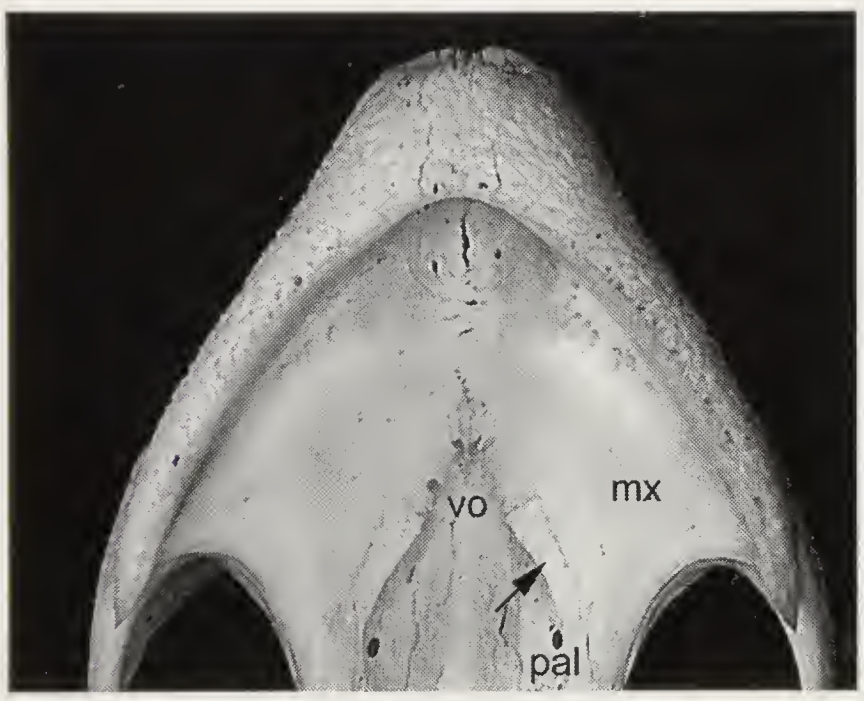

Figure 57. Character 28(1) and 29(0): CAS 228445, *subtrijuga*, ventral view of palate.

Figure 58. Character 29(0): CAS 228419, *amboinensis*, ventral view of palate.

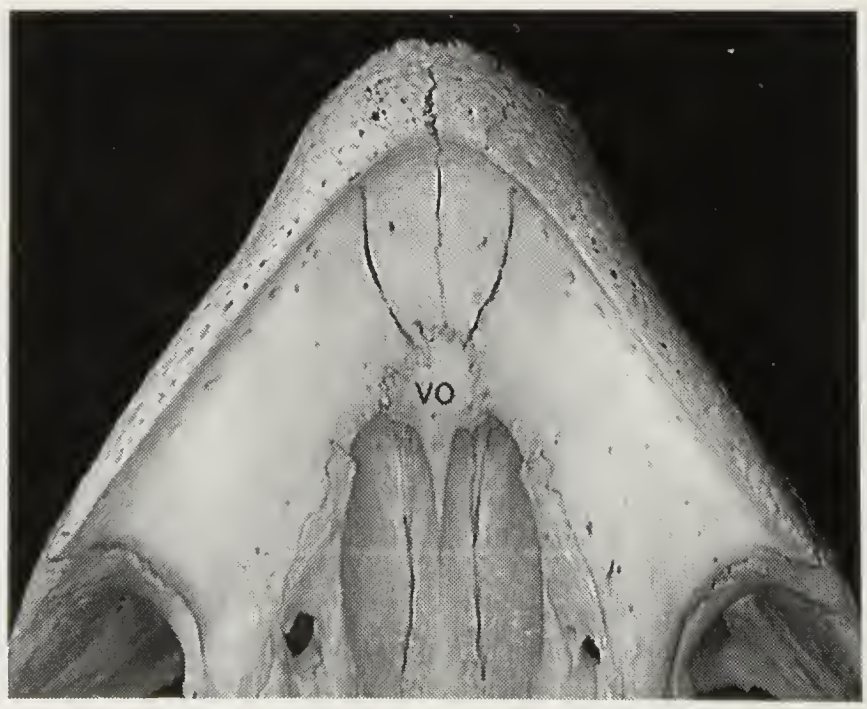

Figure 59. Character 29(1): CAS 228361, *reevesii*, ventral view of palate.

Figure 60. Character 30(0), 31(0), and 32(0): CAS 228447, *orbicularis*, oblique ventral view of palate.

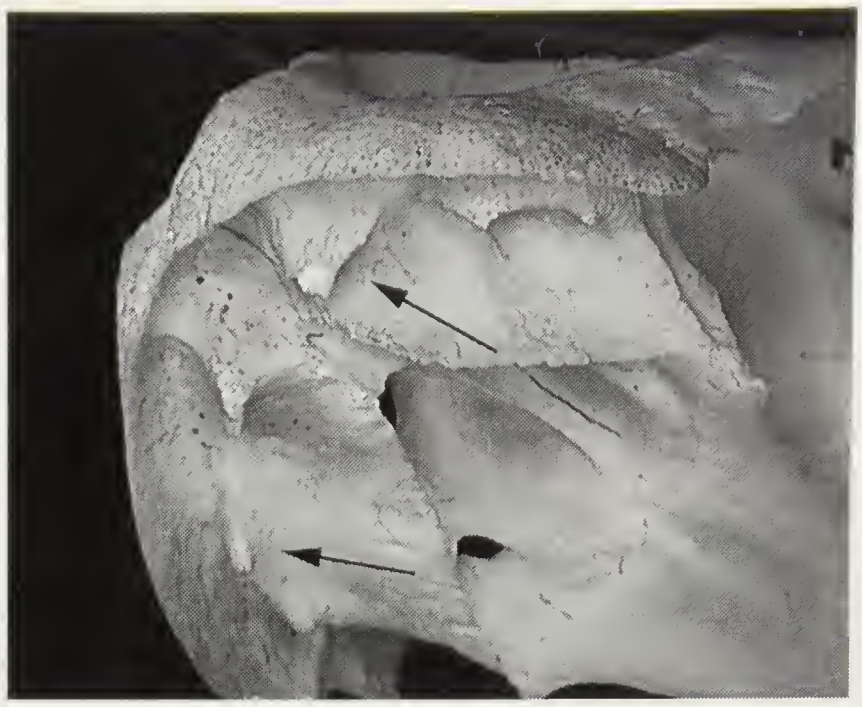

Figure 61. Character 30(1) and 31(1): CAS 228437, *texana*, oblique ventral view of palate.

Figure 62. Character 30(1) and 32(1): TMM 2813, *berlandieri*, ventral view of palate.

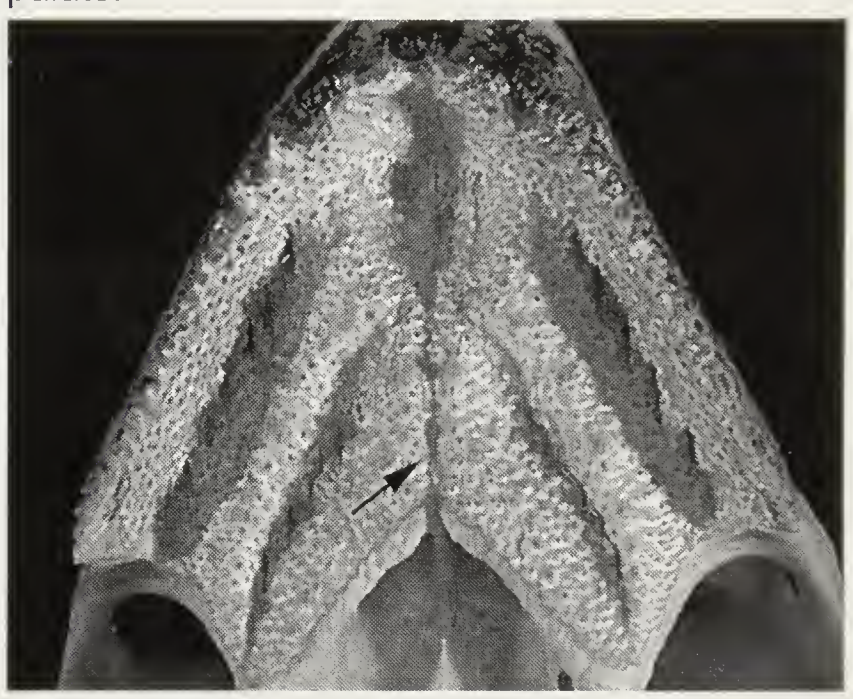

Figure 63. Character 32(2): CM 124246, *petersi*, ventral view of palate.

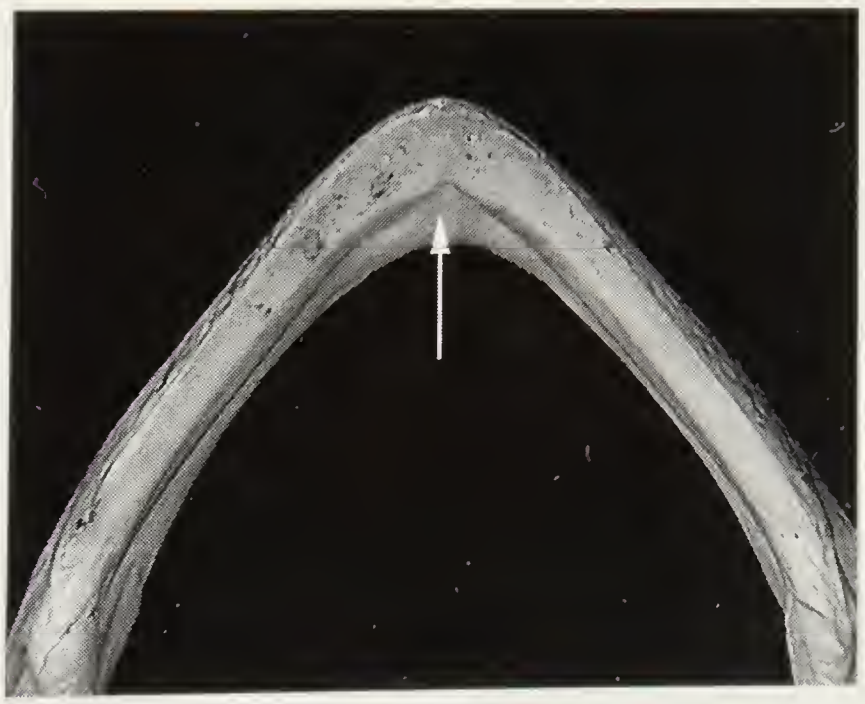

Figure 64. Character 33(0): CAS 228443, *grandis*, dorsal view of mandible.

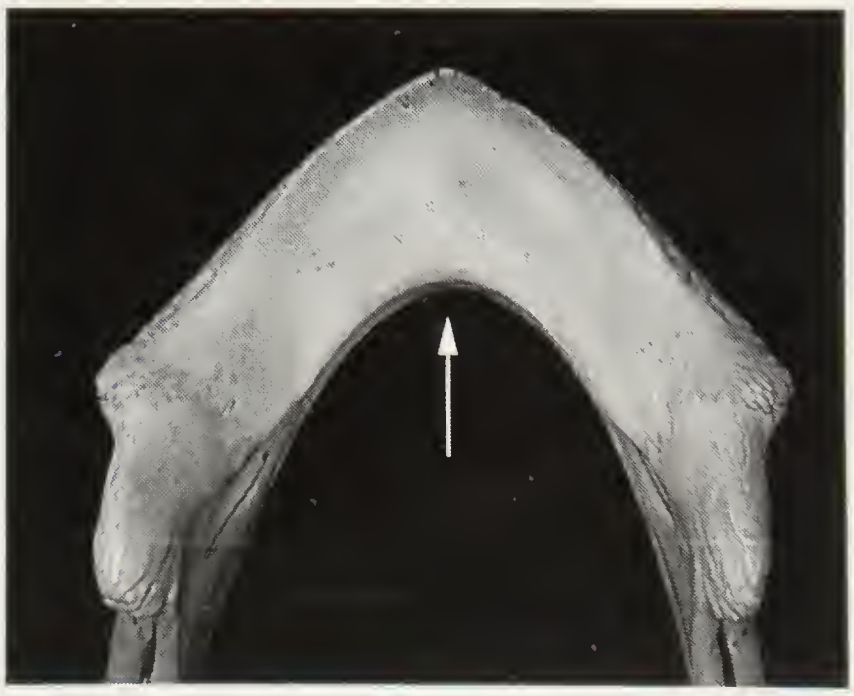

Figure 65. Character 33(1): CAS 228361, *reevesii*, dorsal view of mandible.

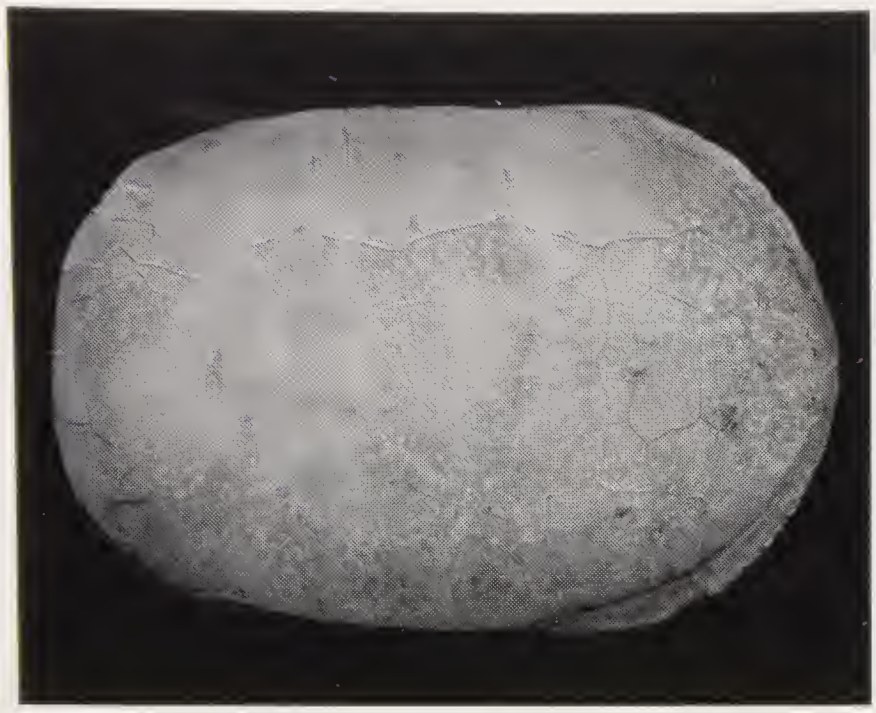

Figure 66. Character 34(0) and 35(0): CAS 228448, *blandingii*, dorsal view of carapace.

Figure 67. Character 34: CAS 228451, *crassicollis*, dorsal view of juvenile carapace showing tricarinae.

Figure 68. Character 34(1) and 35(1): CAS 228444, *mouhotii*, dorsal view of carapace.

Figure 69. Character 36(0): CAS 228376, *galbinifrons*, posterior view of shell.

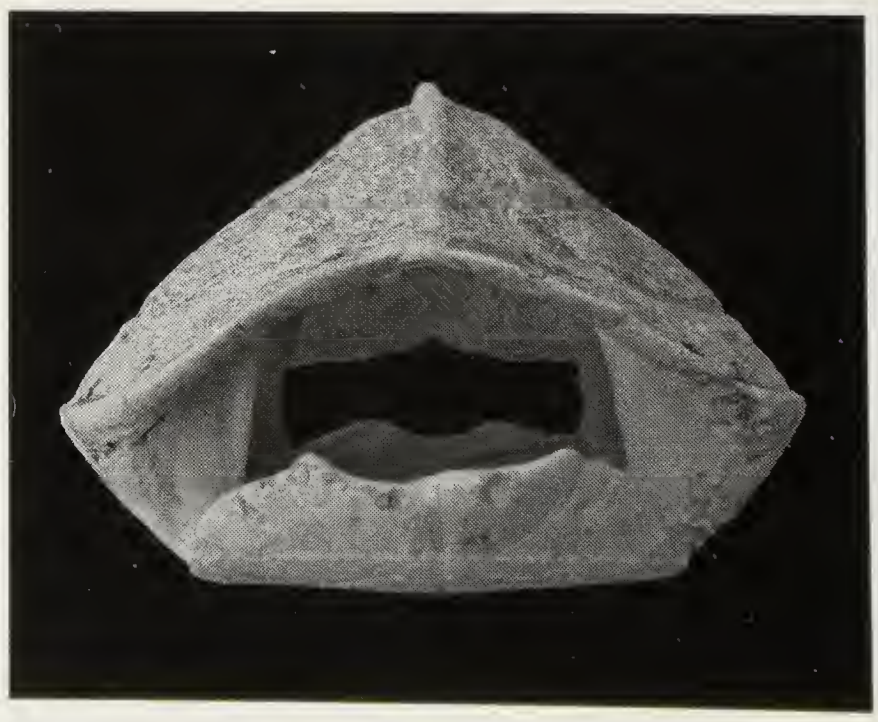

Figure 70. Character 36(1): CM 259430, *tentoria*, anterior view of shell.

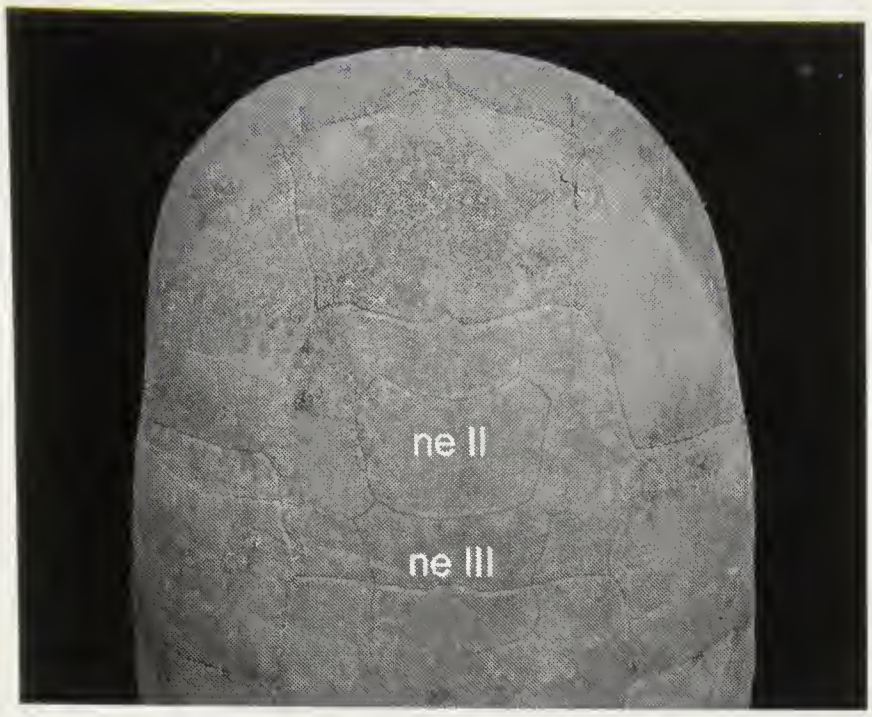

Figure 71. Character 37(0) and 38(0): CAS 228346, *blandingii*, dorsal view of carapace.

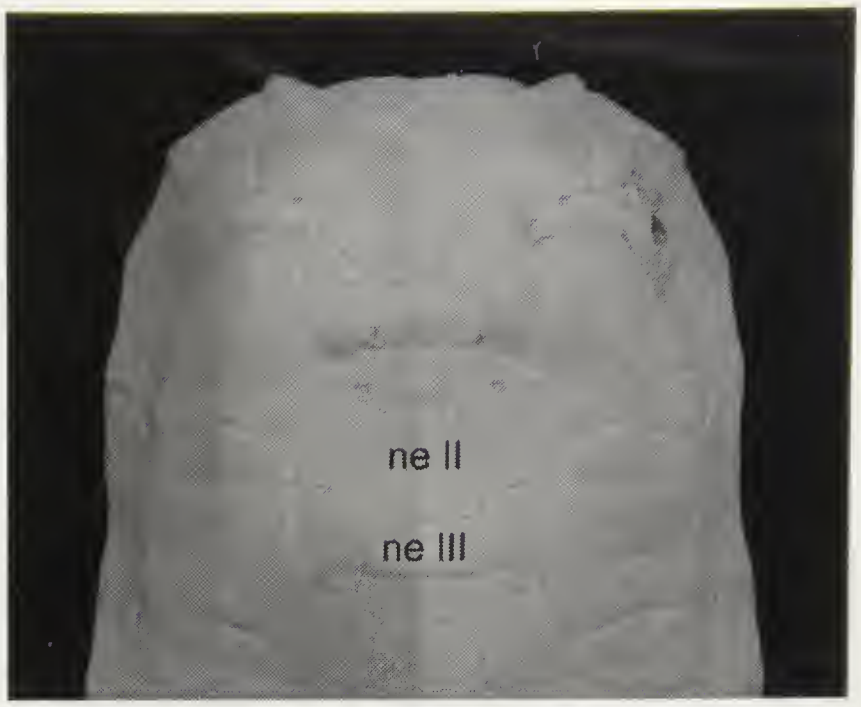

Figure 72. Character 37(1) and 38(1): CAS 228343, *spengleri*, dorsal view of carapace.

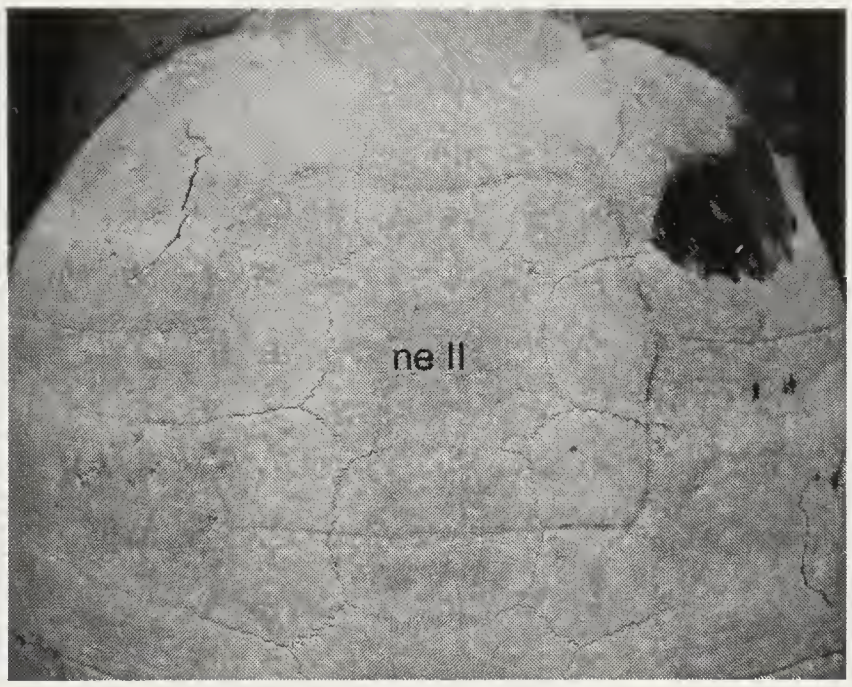

Figure 73. Character 37(2): CAS 228408, *elongata*, dorsal view of carapace.

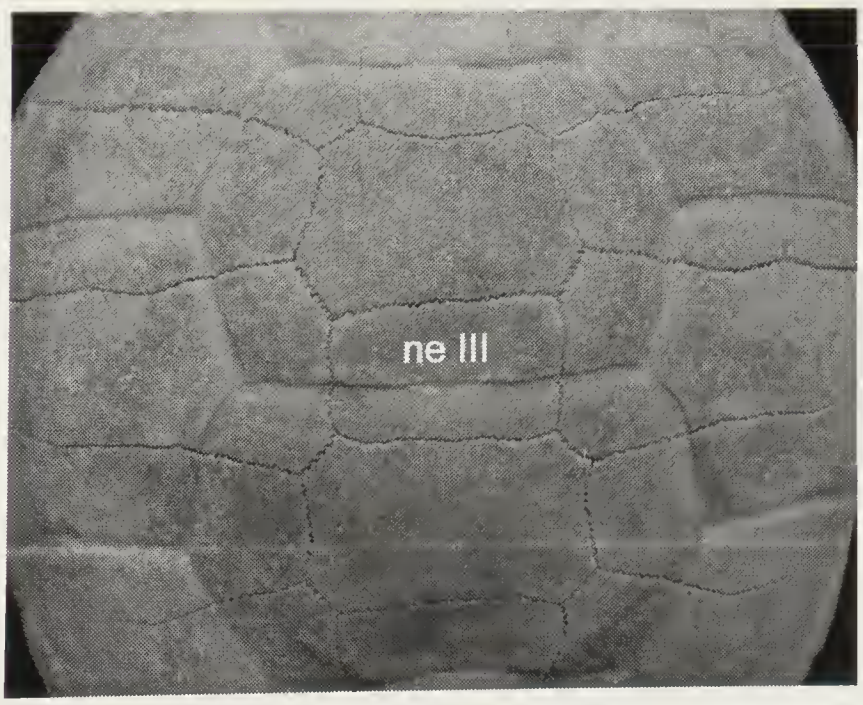

Figure 74. Character 38(2): CAS 228399, *horsfieldi*, dorsal view of carapace.

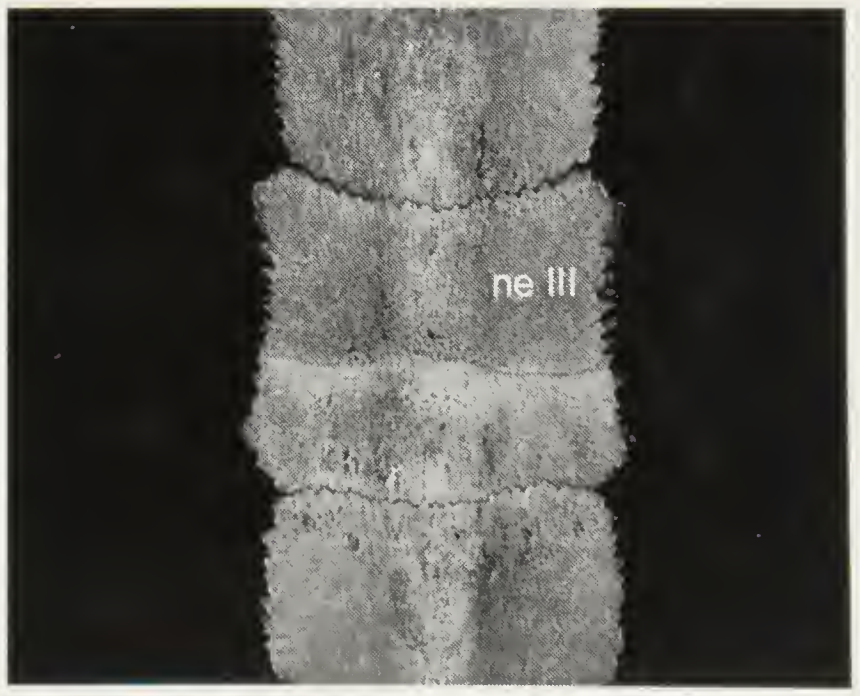

Figure 75. Character 38(3): CAS 228445, *subtrijuga*, dorsal view of neurals II - IV.

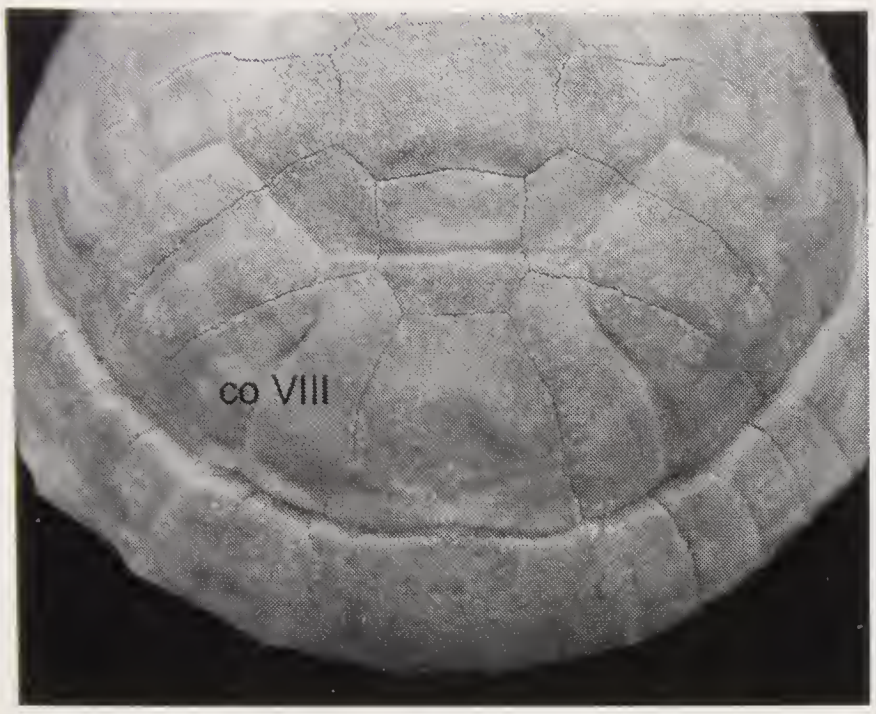

Figure 76. Character 39(0): CAS 228399, *horsfieldi*, posterodorsal view of carapace.

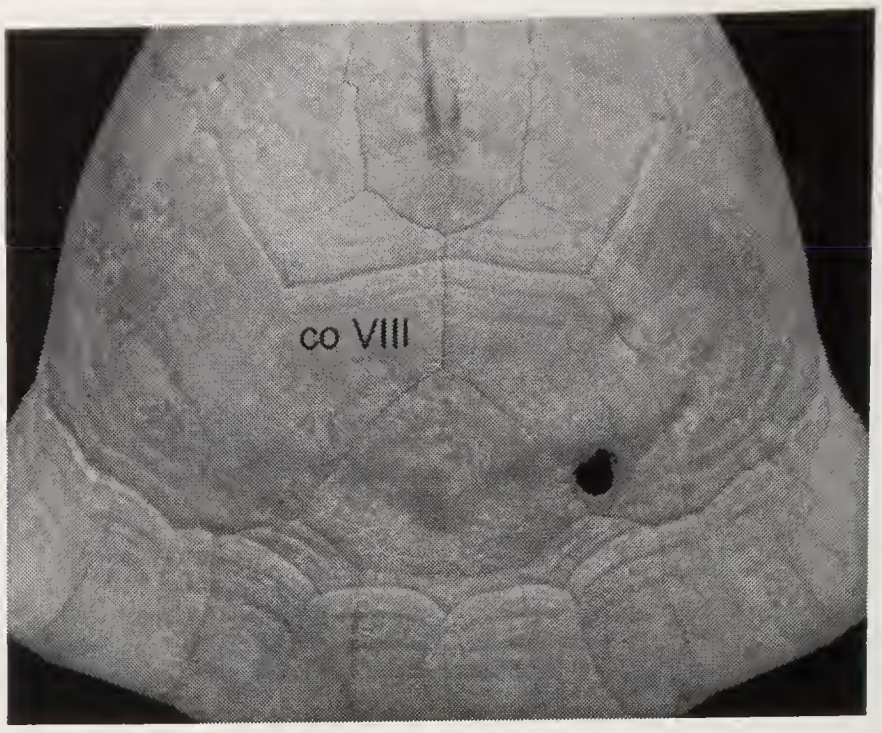

Figure 77. Character 39(1): CAS 228375, *carolina*, posterodorsal view of carapace.

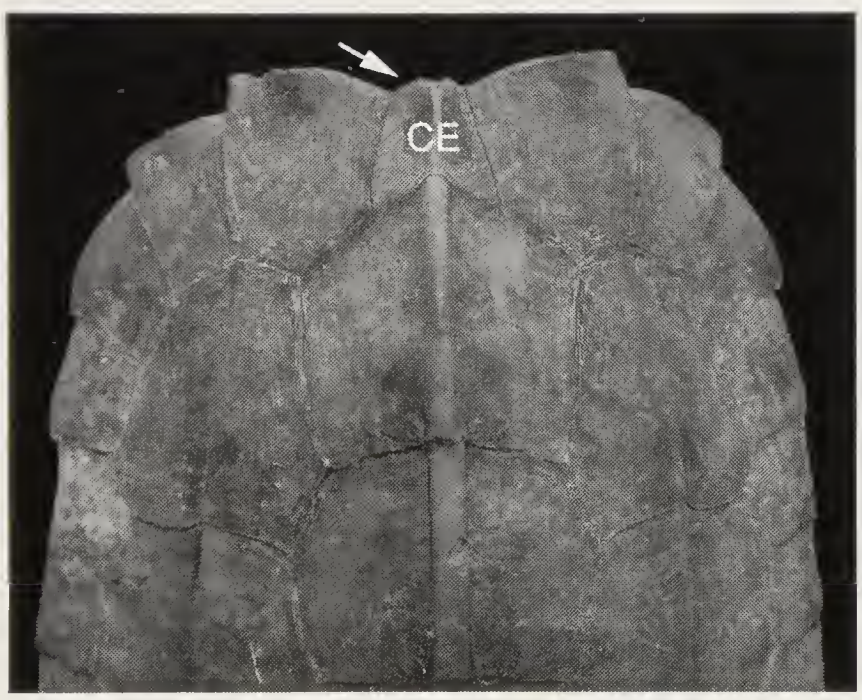

Figure 78. Character 40(0): CAS 228371, *spengleri*, dorsal view of carapace.

Figure 79. Character 40(1): CAS 228430, *carbonaria*, anterodorsal view of carapace.

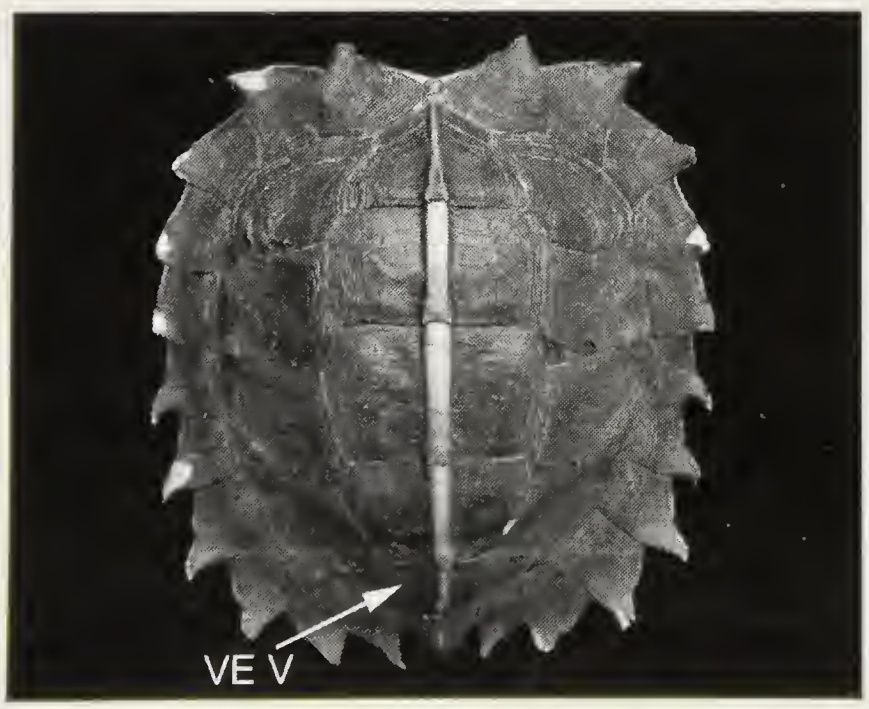

Figure 80. Character 41(0): CAS 228368, *spinosa*, dorsal view of carapace.

Figure 81. Character 41(1): CAS 228450, *N. platynota*, dorsal view of carapace.

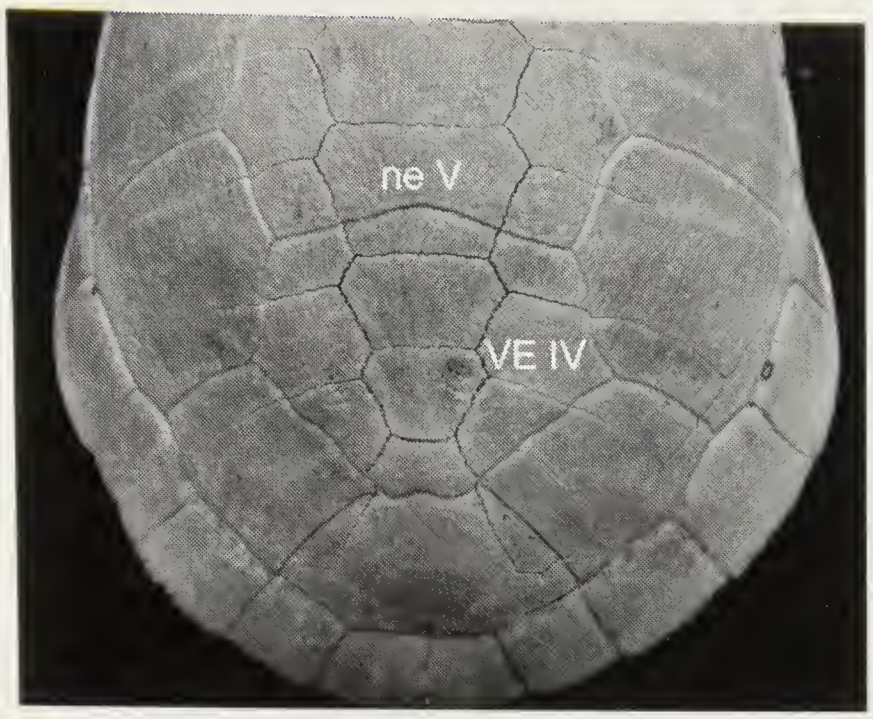

Figure 82. Character 42(0): CAS 228338, *reticularia*, posterodorsal view of carapace.

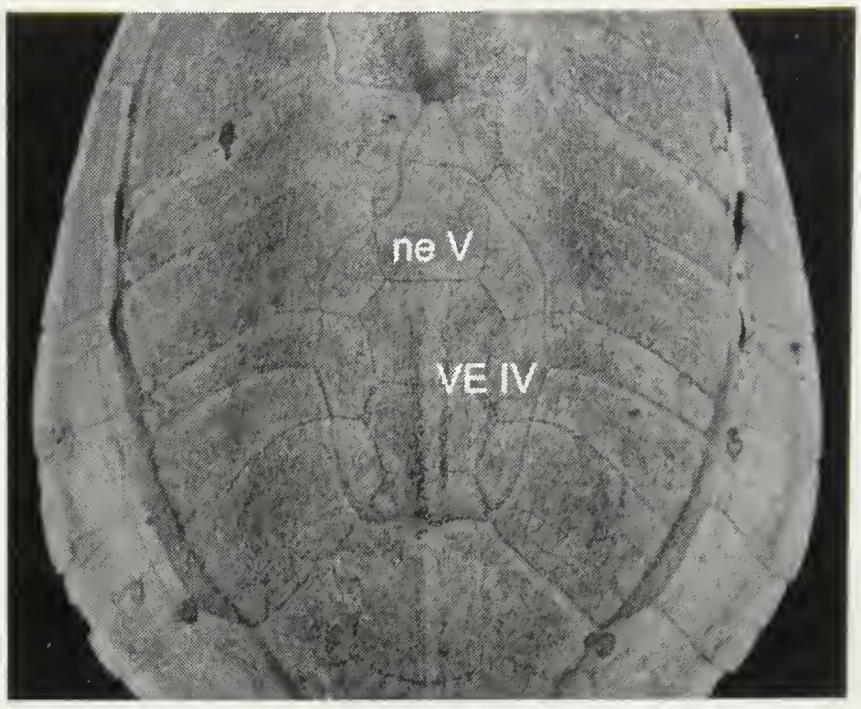

Figure 83. Character 42(1): FMNH 259430, *tentoria*, posterodorsal view of carapace.

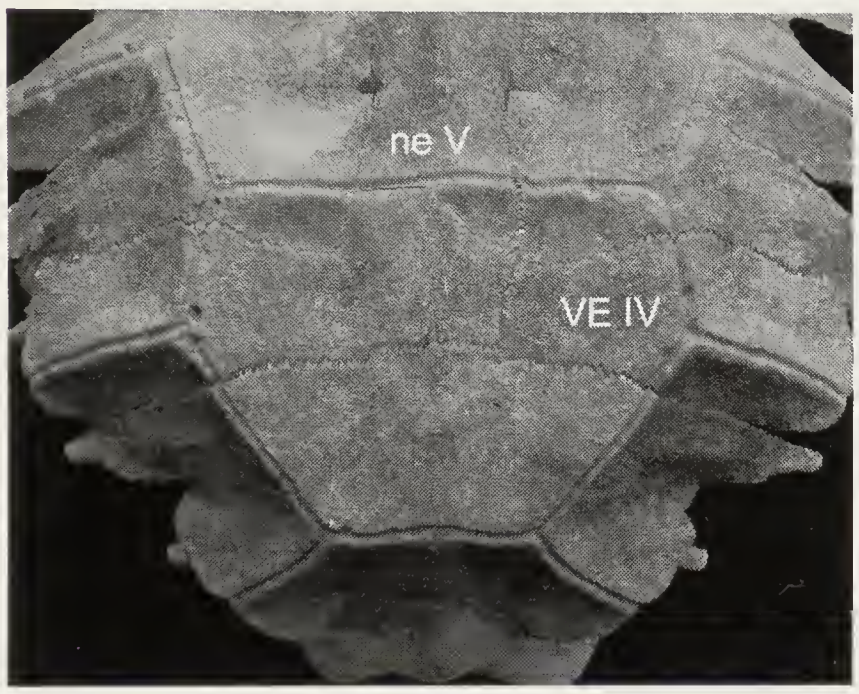

Figure 84. Character 42(2): CAS 228344, *emys*, posterodorsal view of carapace.

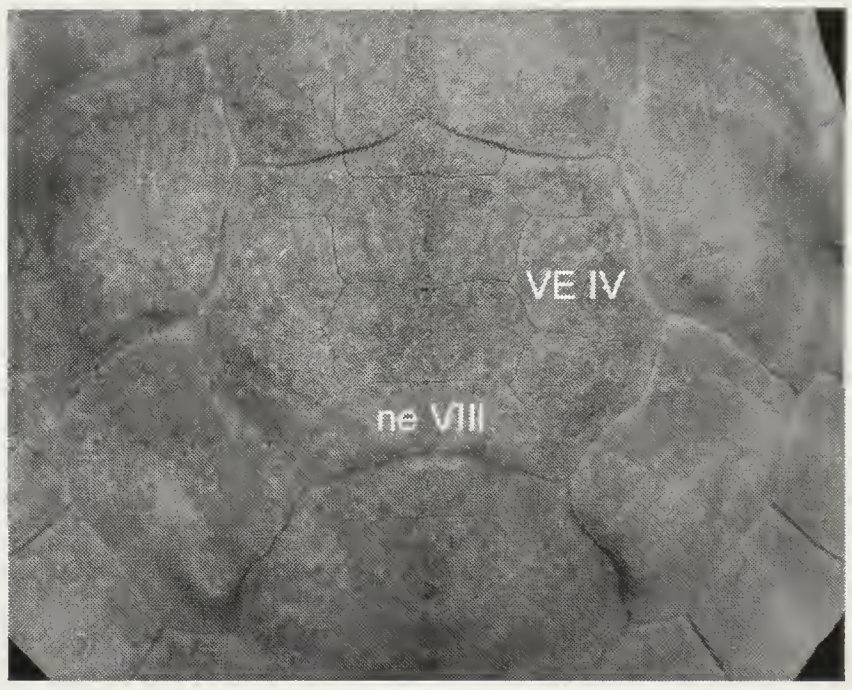

Figure 85. Character 43(0): CAS 228413, *insculpta*, posterodorsal view of carapace.

Figure 86. Character 43(1): YPM 14678, *platynota*, posterodorsal view of carapace.

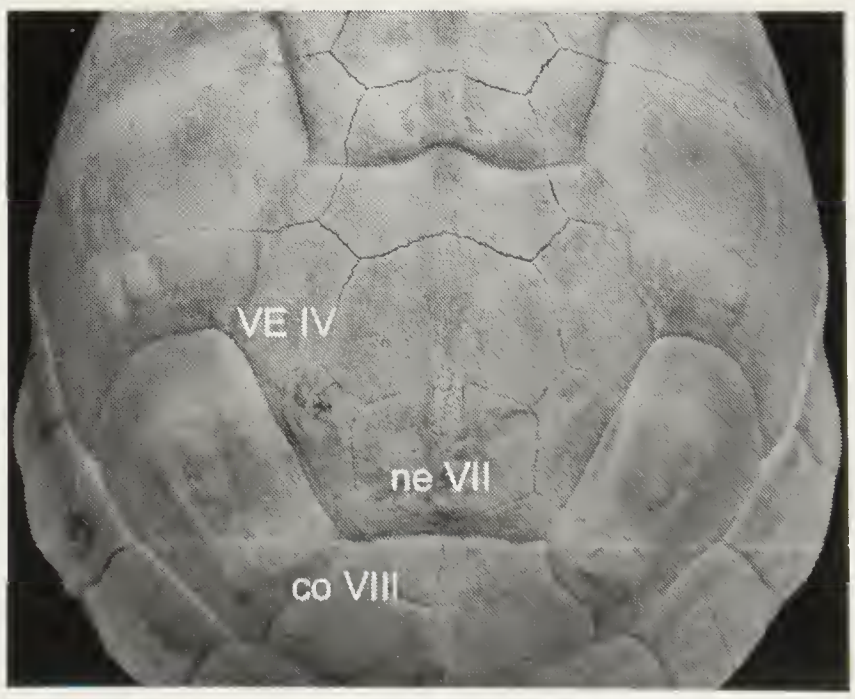

Figure 87. Character 43(2): CAS 228345, *amboinensis*, posterodorsal view of carapace.

Figure 88. Character 44(0): CAS 228368, *spinosa*, dorsal view of carapace.

Figure 89. Character 44(1): CAS 228335, *crassicollis*, dorsal view of carapace.

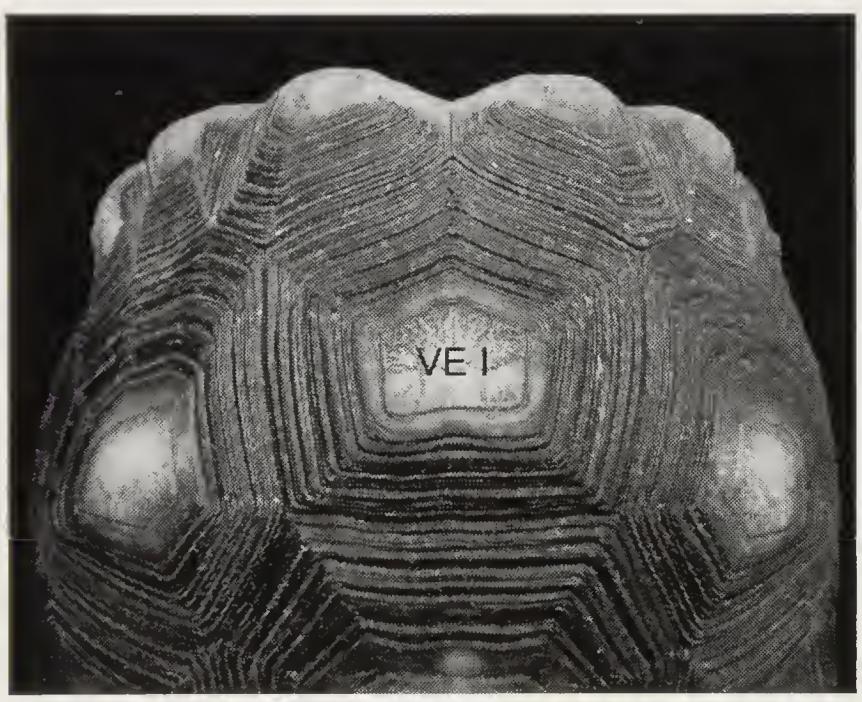

Figure 90. Character 45(0): CAS 228430, *carbonaria*, anterodorsal view of carapace.

Figure 91. Character 45(1): CAS 228341, *grandis*, dorsal view of first vertebral scute, anterior to top.

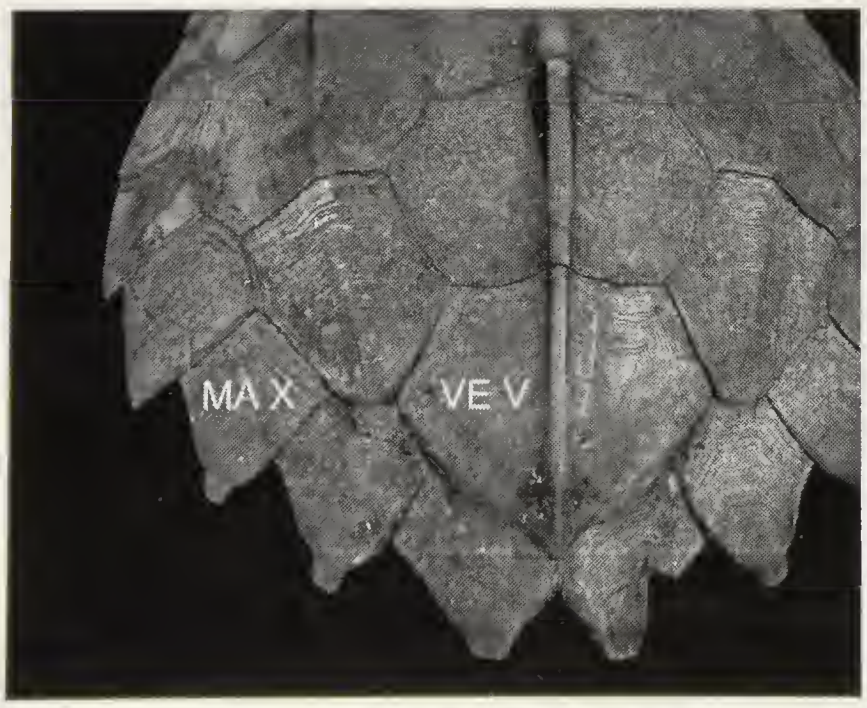

Figure 92. Character 46(0): YPM 11653, *spengleri*, posterodorsal view of carapace.

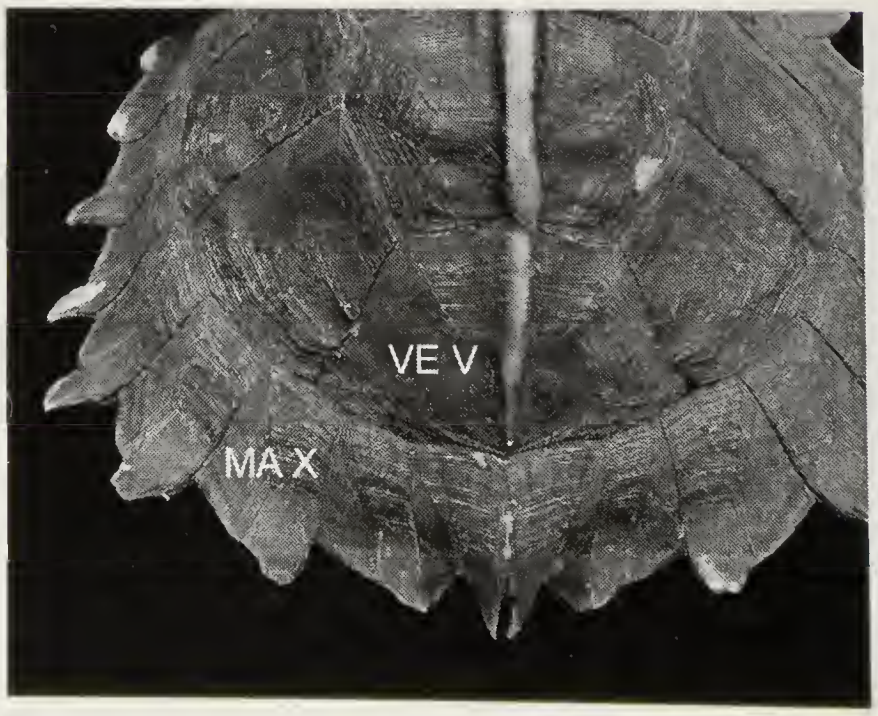

Figure 93. Character 46(1): CAS 228368, *spinosa*, posterodorsal view of carapace.

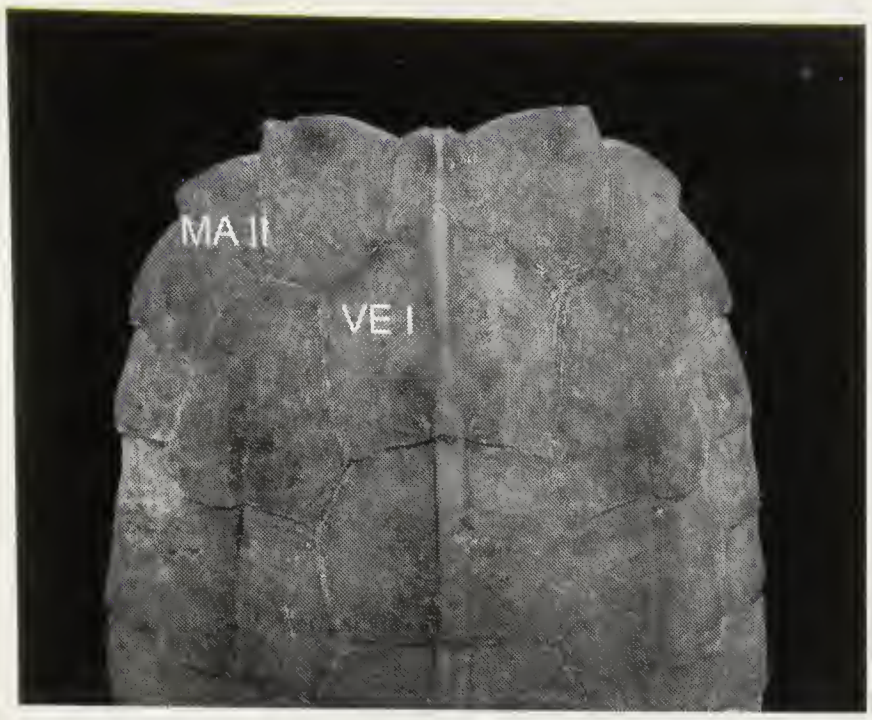

Figure 94. Character 47(0): CAS 228371, *spengleri*, dorsal view of carapace.

Figure 95. Character 47(1): YPM 10382, *blandingii*, dorsal view of carapace.

Figure 96. Character 48(0): CAS 228450, *N. platynota*, left dorsolateral view of carapace.

Figure 97. Character 48(1): CAS 228430, *carbonaria*, left dorsolateral view of carapace.

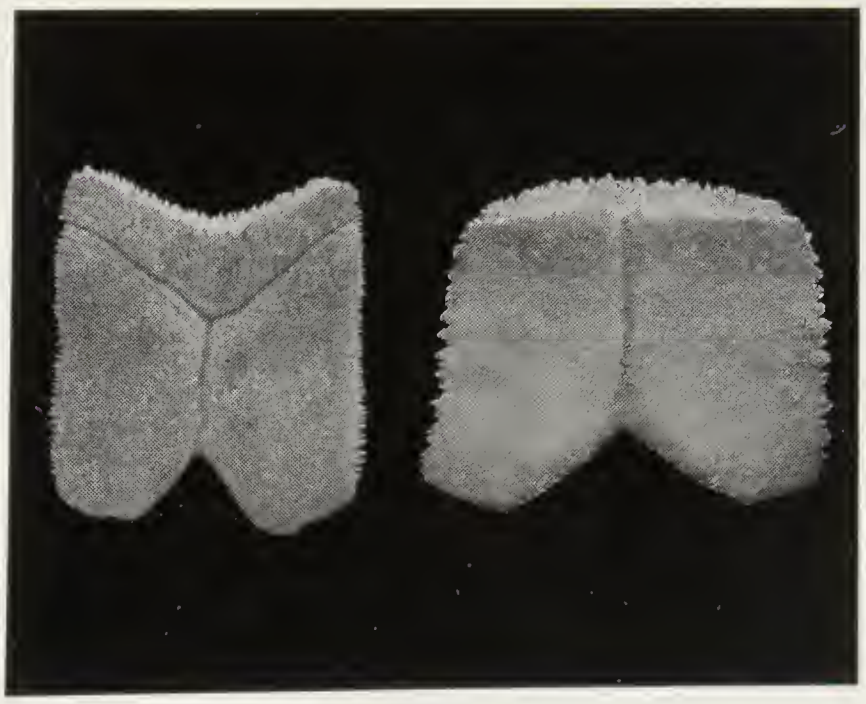

Figure 98. Character 49(0): CAS 228458, *texana* (left); 49(1): CAS 228341, *grandis* (right); dorsal view of pygals.

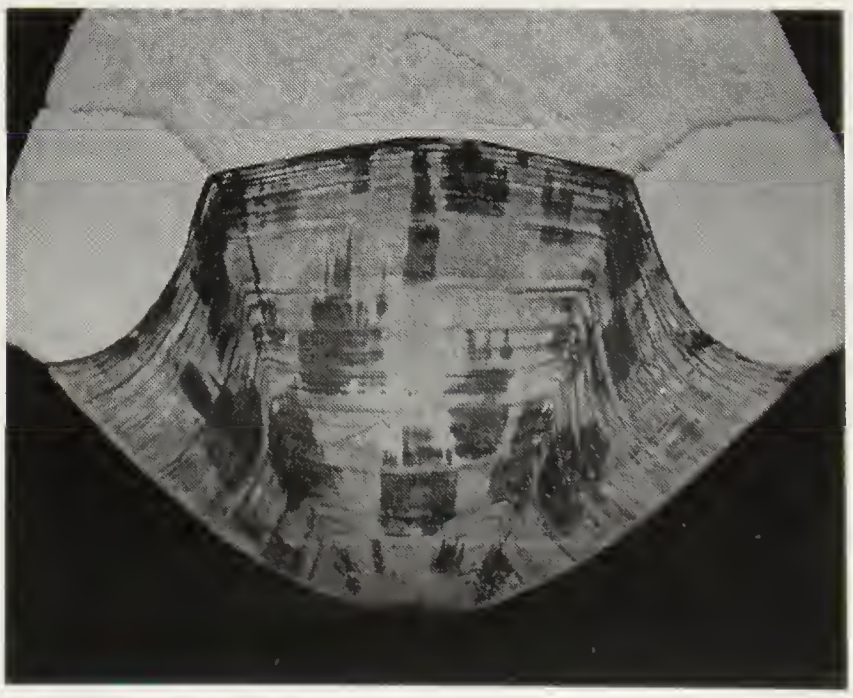

Figure 99. Character 49(2): CAS 228449, *pardalis*, posterior view of carapace.

Figure 100. Character 50(0): CAS 228399, *horsfieldi*, lateral view of carapace.

Figure 101. Character 50(1): CAS 228375, *carolina*, lateral view of carapace.

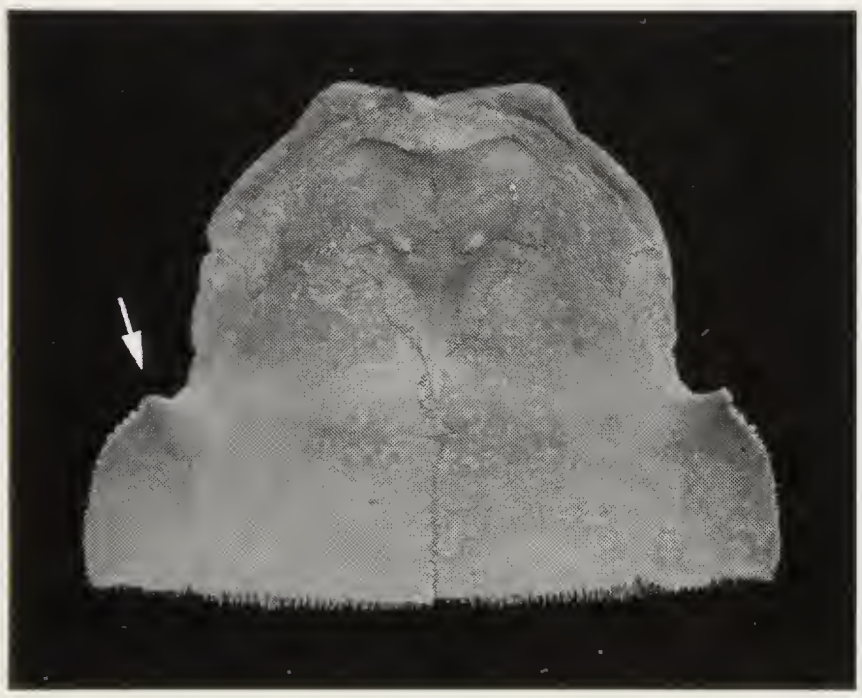

Figure 102. Character 51(0): CAS 228342, *platynota*, ventral view of anterior plastral lobe.

Figure 103. Character 51(1): CAS 228419, *amboinensis*, ventral view of anterior plastral lobe.

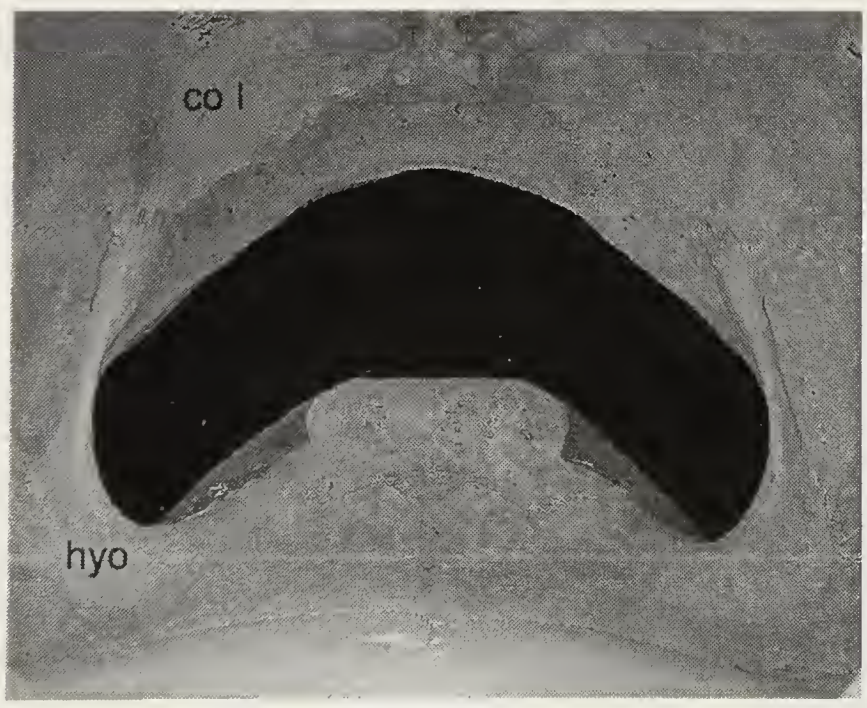

Figure 104. Character 51(2): CAS 228408, *elongata*, internal view of shell from posterior.

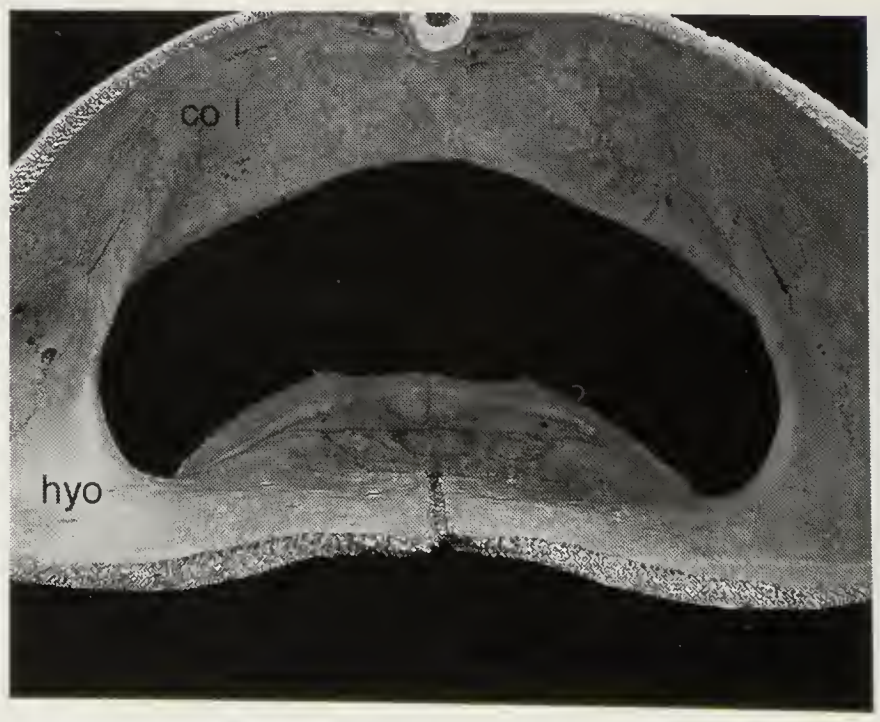

Figure 105. Character 51(3): CAS 228406, *insculpta*, internal view of shell from posterior.

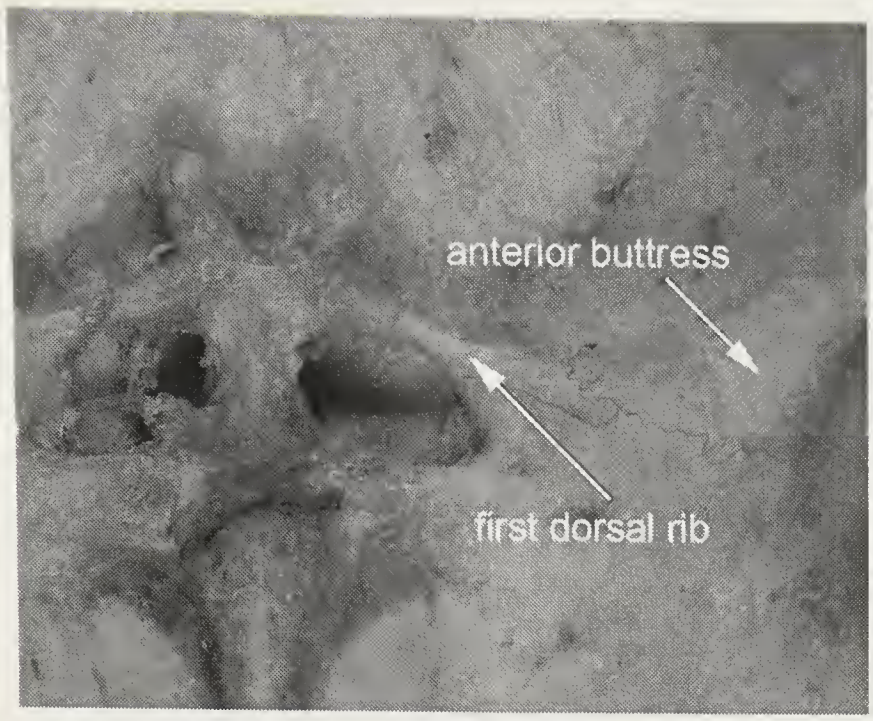

Figure 106. Character 51(4): YPM 14073, *thurjii*, left ventral view of first thoracic rib.

Figure 107. Character 52(0): YPM 691, *carolina*, ventral view of posterior plastral lobe.

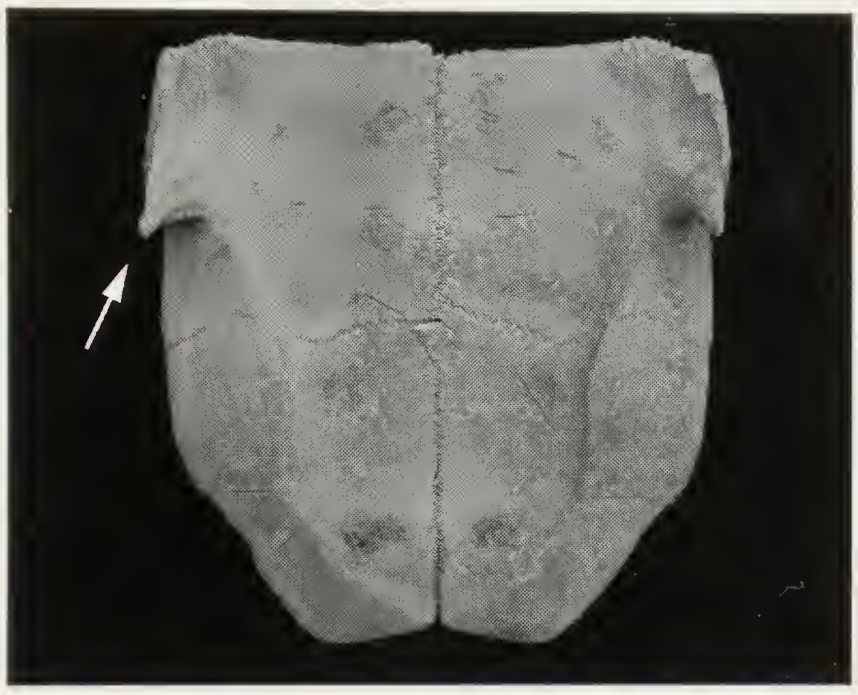

Figure 108. Character 52(1): CAS 228434, *blandingii*, ventral view of posterior plastral lobe.

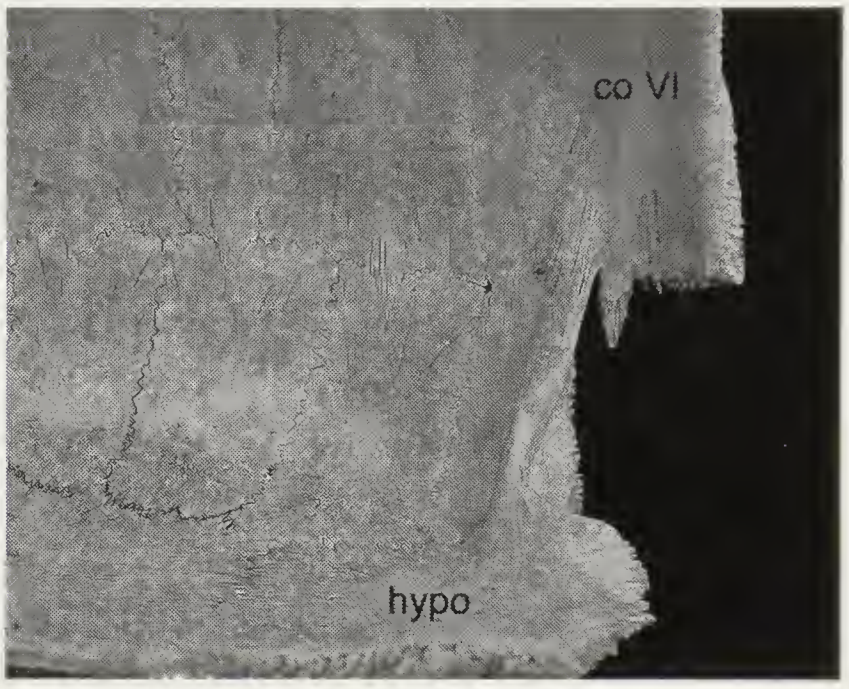

Figure 109. Character 52(2): CAS 228349, *pardalis*, medial view of partial right shell.

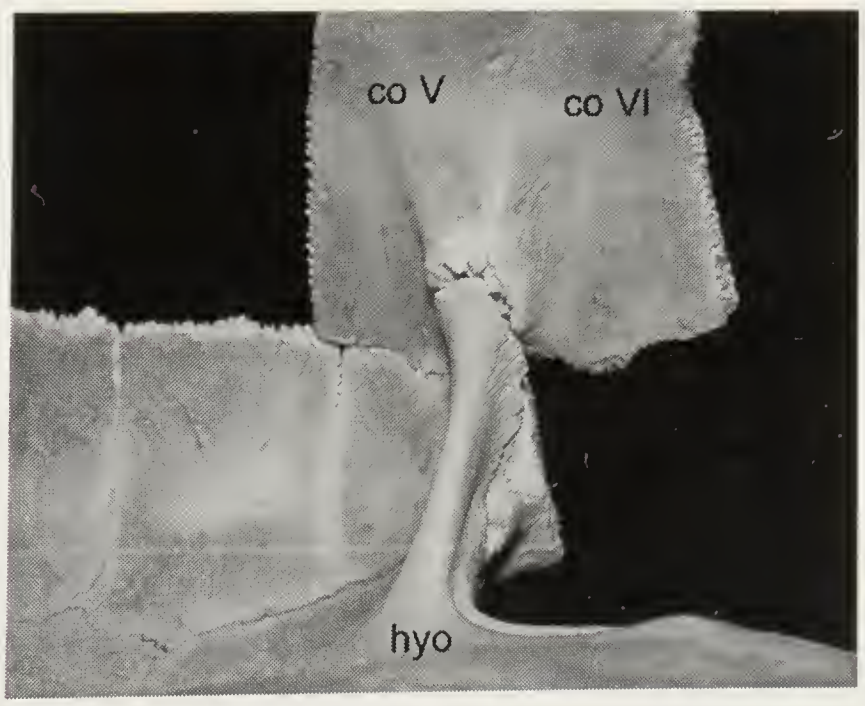

Figure 110. Character 52(3): CAS 228361, *reevesii*, medial view of partial right shell.

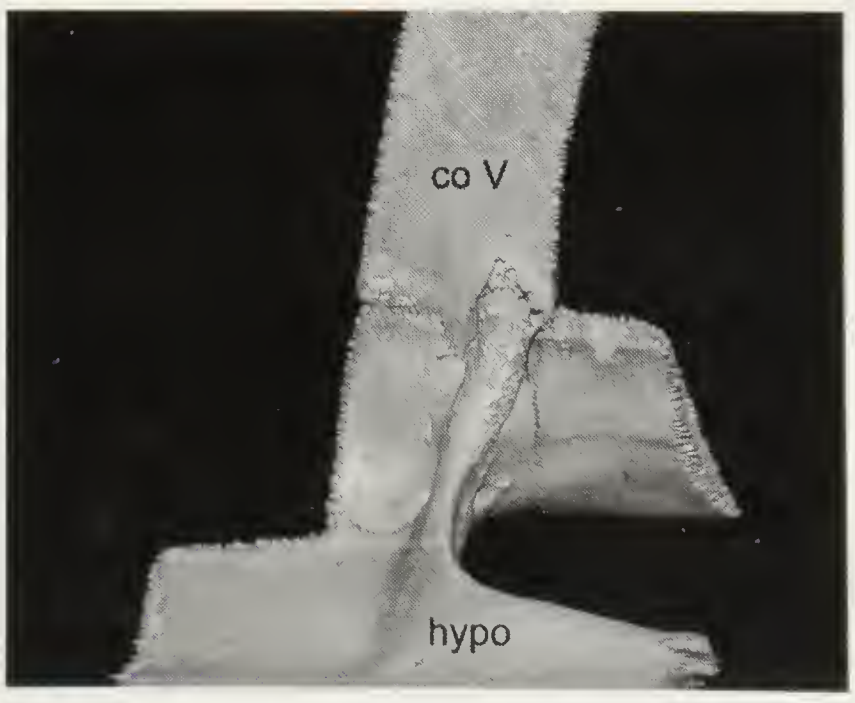

Figure 111. Character 52(4): CAS 228341, *grandis*, medial view of partial right shell.

Figure 112. Character 53(0): CAS 228447, *orbicularis*, ventral view of carapace.

Figure 113. Character 53(1): CAS 228345, *amboinensis* (left); CAS 228373, *blandingii* (right); ventral view of carapaces.

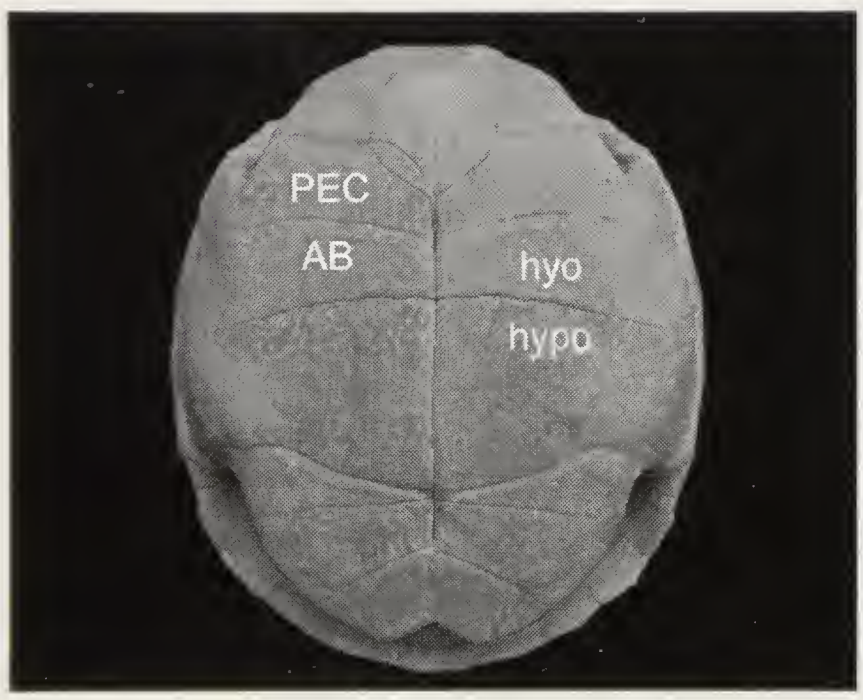

Figure 114. Character 54(0): CAS 228399, *horsfieldi*, ventral view of shell.

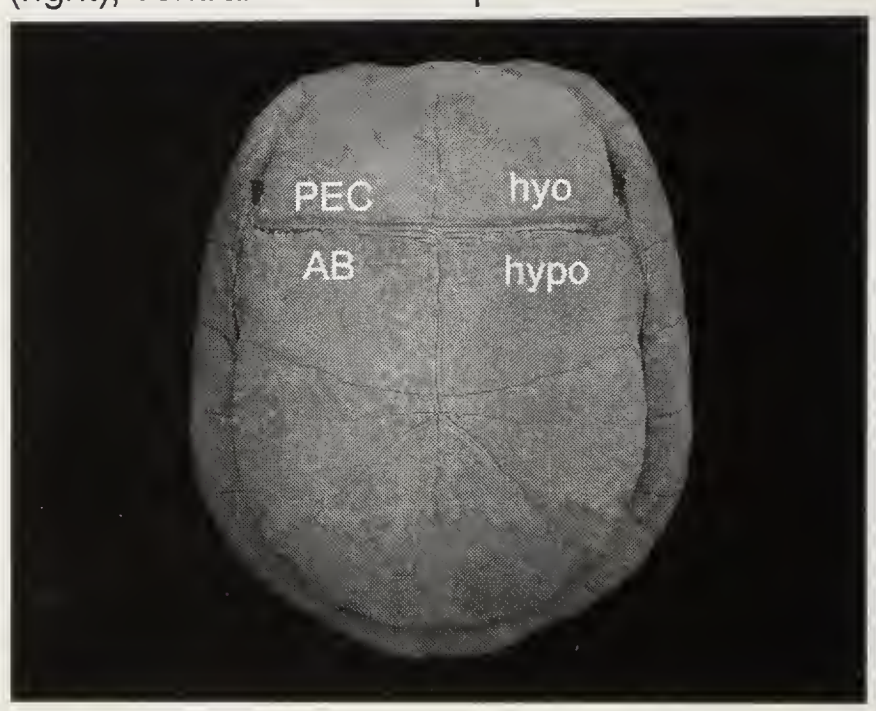

Figure 115. Character 54(1): CAS 228345, *amboinensis*, ventral view of shell.

Figure 116. Character 55(0): CAS 228403, *tornieri*, right posterolateral view of carapace.

Figure 117. Character 55(1): YPM 12653, *erosa*, right posterolateral view of carapace.

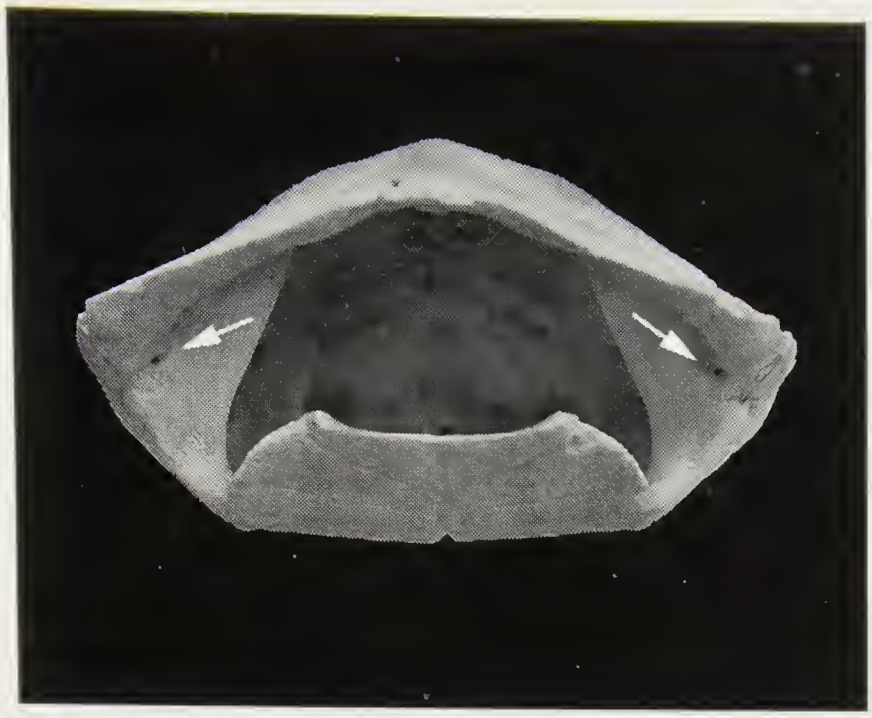

Figure 118. Character 57(0): CAS 228335, *crassicollis*, anterior view of shell.

Figure 119. Character 58(0): CAS 228335, *crassicollis*, posterior view of shell.

Figure 120. Character 59(0): CAS 228416, *impressa*, dorsal view of epiplastra.

Figure 121. Character 59(1): CAS 228397, *carbonaria*, dorsal view of epiplastra.

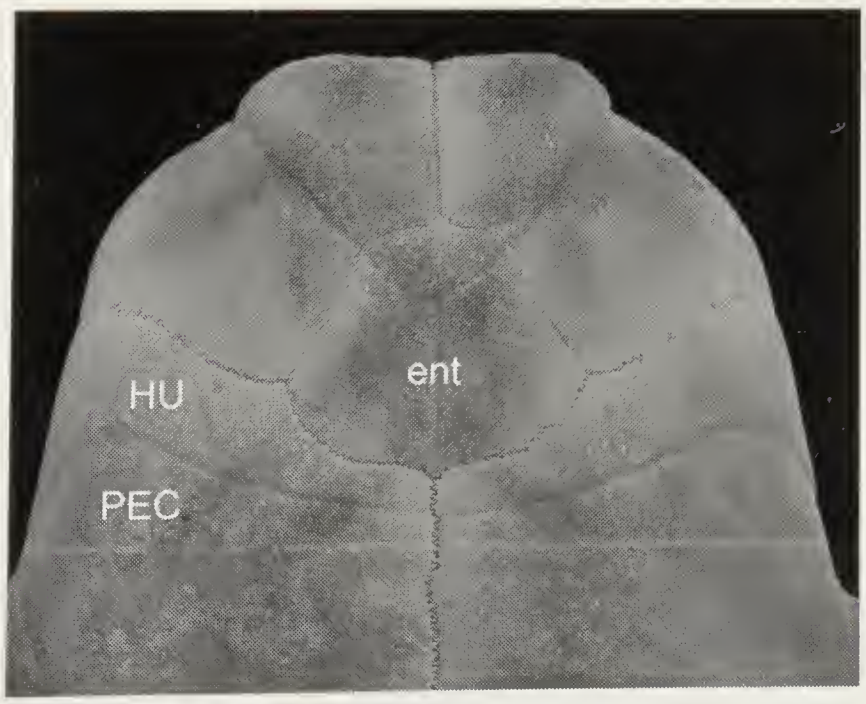

Figure 122. Character 60(0): CAS 228437, *texana*, ventral view of anterior plastral lobe.

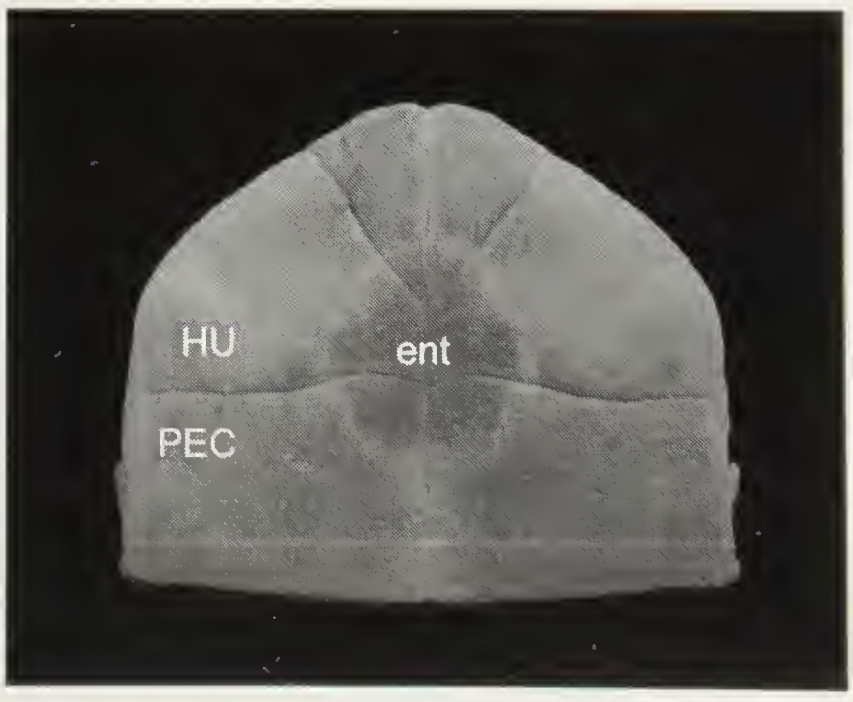

Figure 123. Character 60(1): CAS 228345, *amboinensis*, ventral view of anterior plastral lobe.

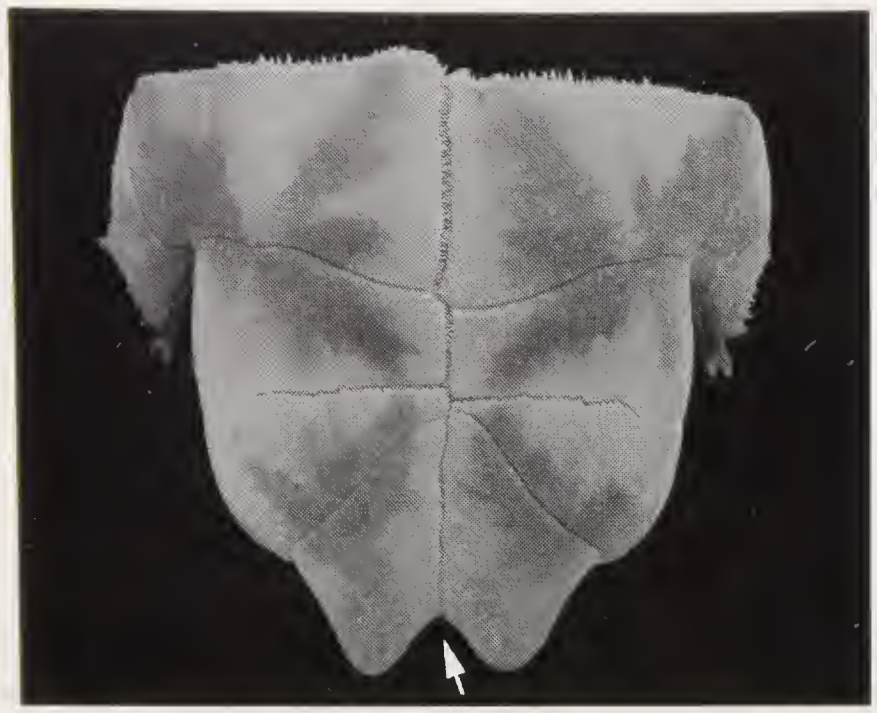

Figure 124. Character 61(0): CAS 228437, *texana*, ventral view of posterior plastral lobe.

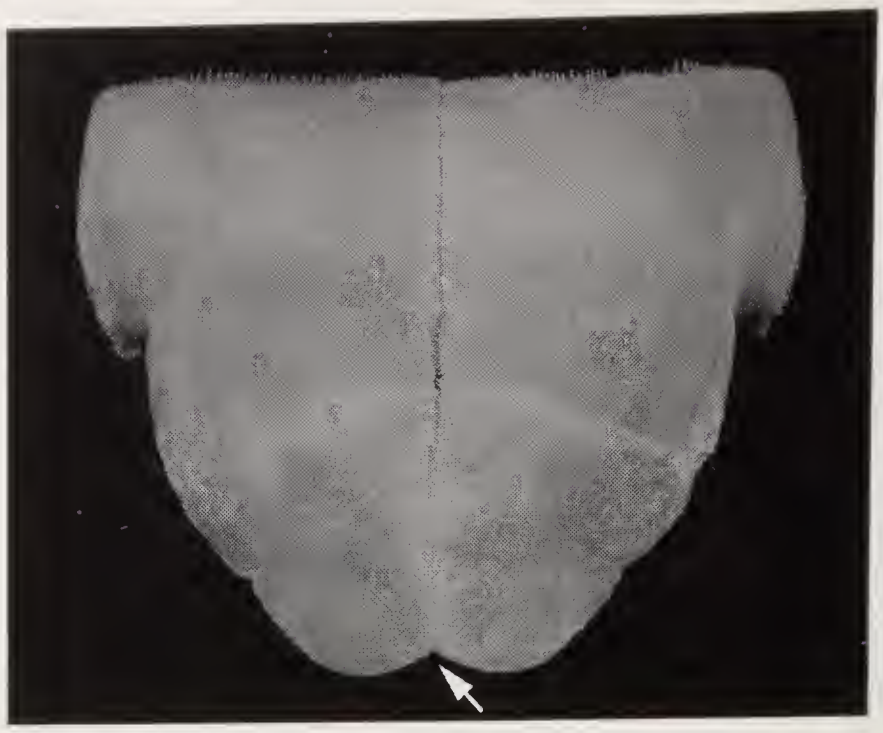

Figure 125. Character 61(1): YPM 14678, *N. platynota*, ventral view of posterior plastral lobe.

Figure 126. Character 61(2): CAS 228376, *galbinifrons*, ventral view of posterior plastral lobe.

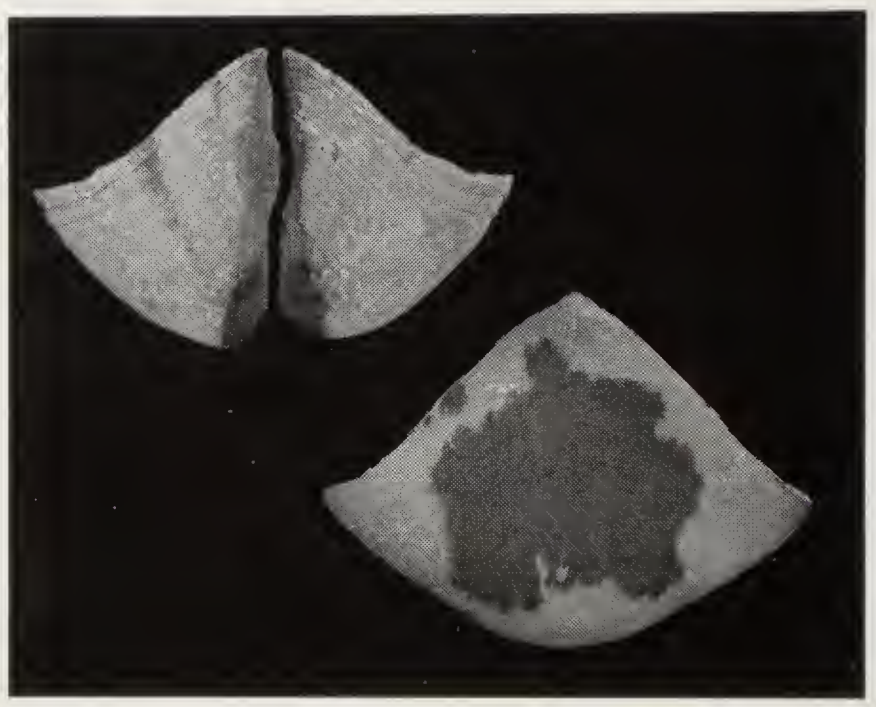

Figure 127. Character 62(0): CAS 228345, *amboinensis* (left); 62(1): CAS 228376, *galbinifrons* (right); ventral view of anal scutes.

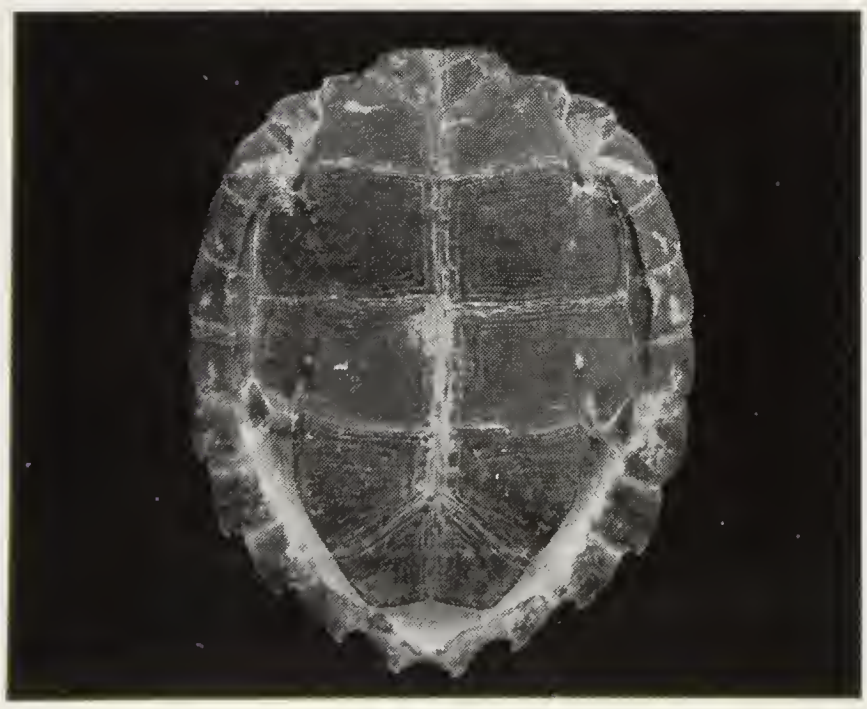

Figure 128. Character 63(0): CAS 228450, *platynota*, ventral view of plastron.

Figure 129. Character 63(1): CAS 228368, *spinosa*, ventral view of plastron.

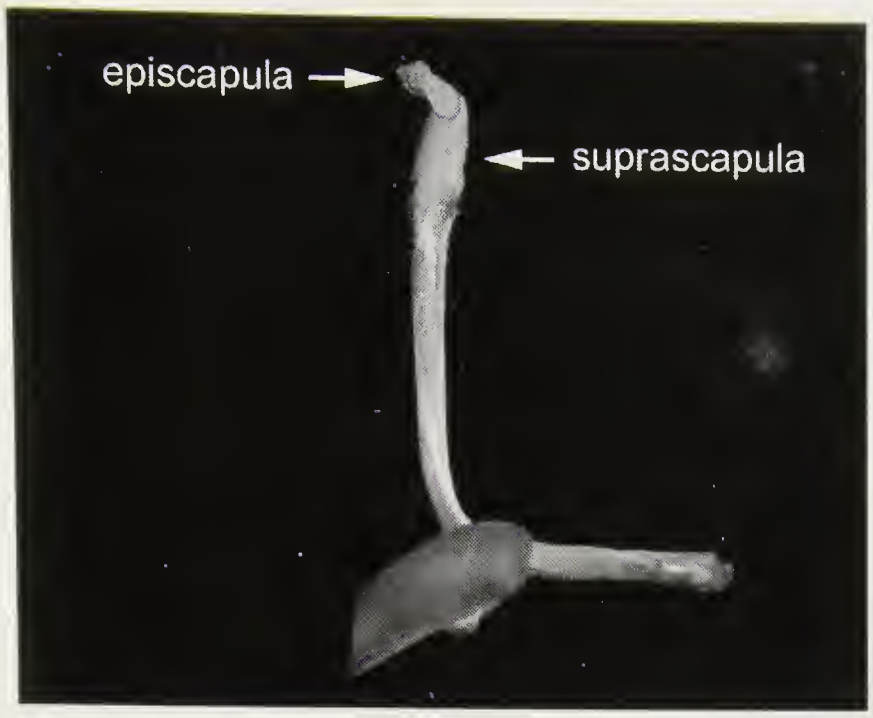

Figure 130. Character 64(1) and 65(1): TNHC 62532, *ornata*, lateral view of right scapulacoracoid.

Figure 131. Character 66(0): CAS 228345, *amboinensis* (left); 66(1): CAS 228397, *carbonaria* (right); coracoids.

Figure 132. Character 67(0) and 68(0): YPM 14677, *blandingii*, top view of lower arm and manus.

Figure 133. Character 67(1) and 68(1): YPM 16450, *horsfieldi*, top view of lower arm and manus.

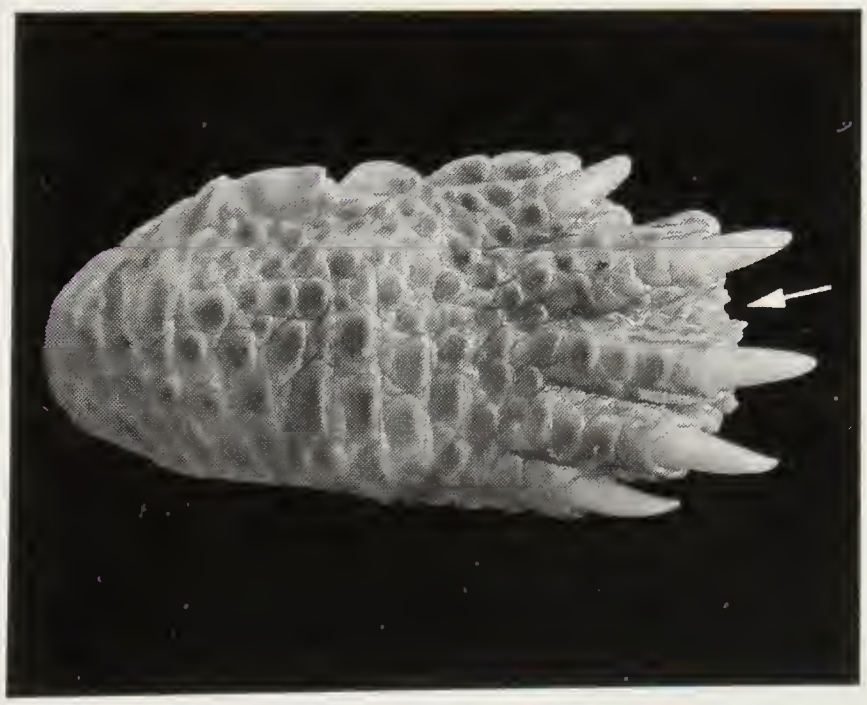

Figure 134. Character 69(0): YPM 2983, *terrapin*, top view of lower arm and manus.

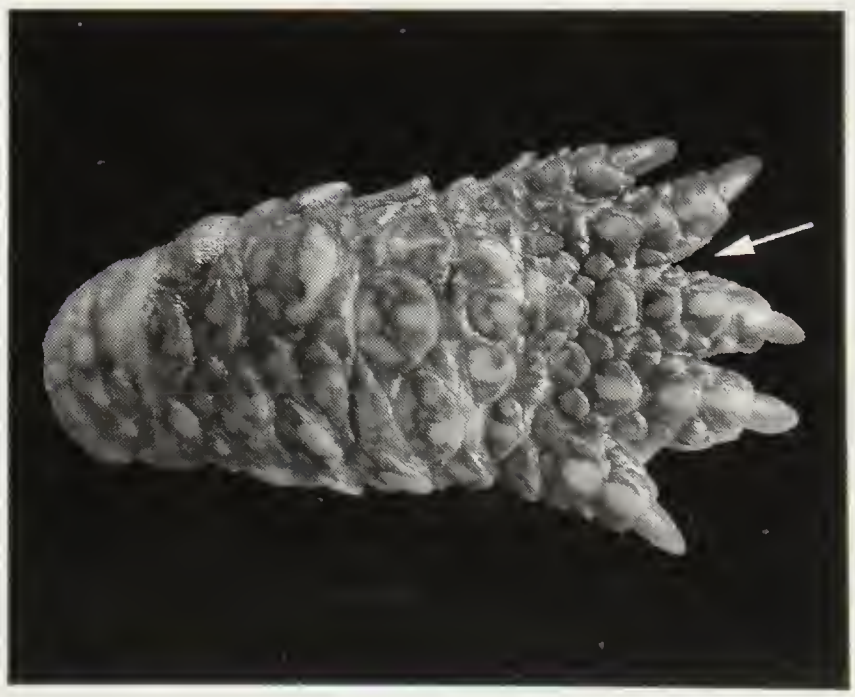

Figure 135. Character 69(1): YPM 14445, *spengleri*, top view of lower arm and manus.

Figure 136. CAS 228348, *punctularia*, right lateral view.

Figure 137. FMNH 224107, *borneoensis*, left anterolateral view of trigeminal foramen.

Figure 138. FMNH 224107, *borneoensis*, right anterolateral view of trigeminal foramen.

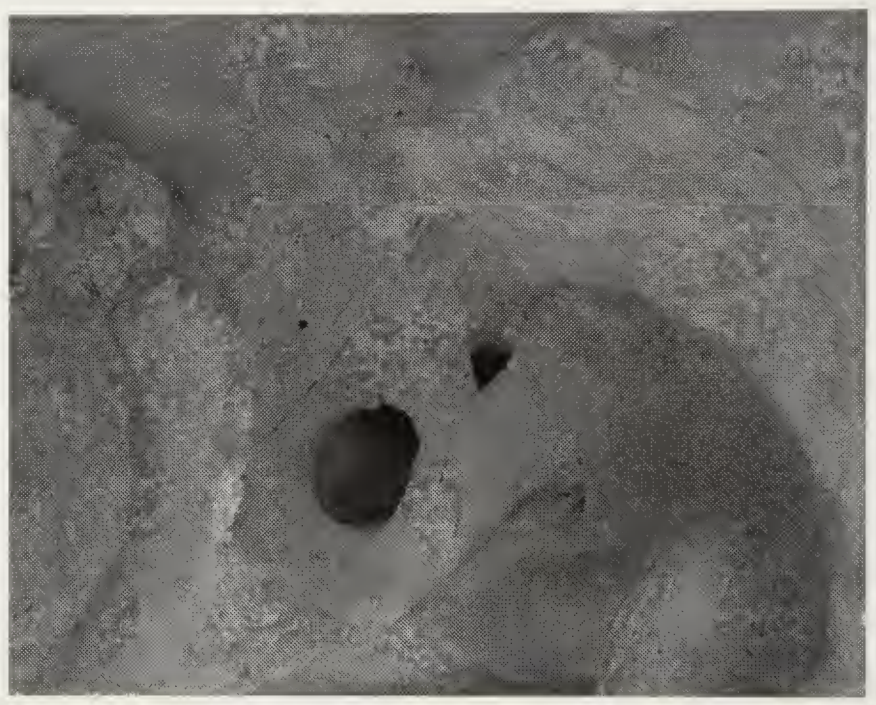

Figure 139. FMNH 224122, *borneoensis*, right anterolateral view of trigeminal foramen.

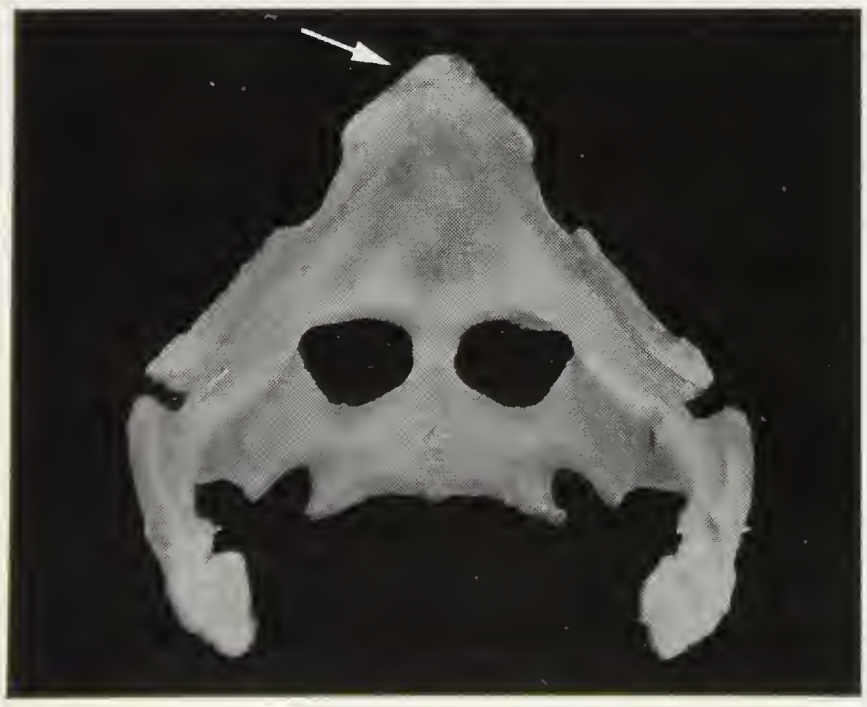

Figure 140. CAS 228378, *carolina*, dorsal view of pelvis.

Figure 141. CAS 228443, *grandis*, posteroventral view of otic region.

As practicing vertebrate paleontologists, we also hope that our efforts here will stimulate additional investigation and publication of the extensive fossil record of testudinoid turtles. Morphology is, of course, of paramount importance for the interpretation of fossils. Our visits to many museums in the last several years revealed an abundance of unpublished testudinoid fossil material. Although a phylogenetic analysis was not a goal of this research, we adopt the convenient and now familiar means of summarizing morphological data by providing a character matrix that summarizes some of our observations. Although character data can be used to assist paleontologists in diagnosing fossil testudinoid specimens, we also encourage paleontologists to utilize our study as a starting point for basic morphologic descriptions. Description of differential diagnostic characters generally is an adequate minimum for the erection of a new taxon. However, such a diagnosis is, in itself, not particularly helpful to systematists trying to score a matrix and place a fossil into a broader phylogenetic context. Descriptions of new fossil specimens (and taxa) will be most useful if they include discussions of character state data for all preserved anatomical regions. This current summary of morphological characters that traditionally are used in systematic treatments of testudinoids can be used as a preliminary guide to the anatomical regions and features that would be most useful when included as part of a description of new fossil material.

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Appendix 1

List of specimens used.

agassizii, CAS 33867, FMNH 216746, FMNH 250843; *alabamensis*, CM 95968, CM 95991; *amboinensis*, CAS 153872, CAS 228345, CAS 228369, CAS 228412, CAS 228419, FMNH 224009; *annandalei*, FMNH 258876, FMNH 258879, FMNH Moll3036; *annulata*, CAS SUR7425, CM 87903, YPM 15410; *arachnoides*, MCZ 54050; *areolatus*, MCZ 42214; *areolata*, CM 47957, CM 87904; *barbouri*, CAS SUR12063, TUMNH 15400, TUMNH 15428, TUMNH 15429, TUMNH 16899; *baska*, FMNH 224095, FMNH 224097, FMNH 224213, FMNH 224124, FMNH 224226; *bealei*, CM 118554, FMNH 255270, FMNH 226542; *belliana*, CAS 228394, CAS 228404; *berlandieri*, TNHC 2813; *blandingii*, CAS 12837, CAS 228346, CAS 228373, CAS 228434, CAS 228448, YPM 14677, YPM 10382; *borneensis*, FMNH 224001, FMNH 224003, FMNH 224004, FMNH 224005, FMHH 224140; *borneoensis*, FMNH 224107, FMNH 224122, FMNH 224129, FMNH 251499, MCZ 42198; *carbonaria*, CAS 228397, CAS 228411, CAS 228427, CAS 228430; *caretta*, CAS 8383, FMNH 31021; *carolina*, CAS 228375, CAS 228378; *caspica*, CAS 141118, CM 118517, FMNH 19714, FMNH 74505, FMNH 98764; *chilensis*, CM 112252; *coahuila*, KU 46929, KU 92623, MCZ 120335; *crassicollis*, CAS 228335, CAS 228451, FMNH 11091, MCZ 7821, MCZ 134451; *decorata*, CM 118590; *dentata*, CAS 134332, KU 47170, MCZ 29567, CAS 228333, CAS 228362, CAS 228414; *elegans*, CAS 228396; *elongata*, CAS 228408, FMNH 183740, FMNH 257382; *emys*, CAS 228344, FMNH 63749, FMNH 224034; *ernsti*, TUMNH 13460, TUMNH 13462, TUMNH 16899; *erosa*, YPM 12653; *flavimaculata*, TUMNH 15375, TUMNH 15404, TUMNH 15747, TUMNH 15787; *flavomarginata*, CAS 18040, CAS 228356, CAS 228357, CAS 228359, FMNH 216515; *flavomarginatus*, MCZ 164926; *forsteni*, CAS 228433; *galbinifrons*, CAS 228358, CAS 228360, CAS 228367, CAS 228376, YPM 14074, YPM 14080; *geographica*, CAS 12809, TUMNH 15391, TUMNH 15392, TUMNH 15410, TUMNH 15430; *geometricus*, MCZ 32184; *gibba*, CAS 228392; *graeca*, CAS 217732, CAS 228435, LMNH 54855, LMNH 54861; *grandis*, CAS 228341, CAS 228443, FMNH 224038, YPM 15431; *guttata*, CAS 8696, CAS 228372, CAS 228386, FMNH 211573; *hamiltonii*, MCZ 120333, YPM 10399; *hermanni*, CAS 228400, CAS 228401, CAS 228402; *homeana*, CAS 228409, CAS 228423, CAS 228428, CAS 228429, CAS 228455, FMNH 19794; *horsfieldi*, CAS 120707, CAS 228398, CAS 228399, CAS 228421, CAS 228425, YPM 16450; *impressa*, CAS 228416; *G. insculpta*, CAS 228406, CAS 228407, CAS 228413; *japonica*, YPM 15482, YPM 15486; *kachuga*, FMNH 224128, FMNH 224152; *kleinmanni*, CAS 228422, CAS 228426, CAS 228431; *kohnii*, TUMNH 10237, TUMNH 12121, TUMNH 14544, TUMNH 15678; *leprosa*, CM 137031; *marmorata*, CAS no number, CAS 188533, CAS 220052, FMNH 22076; *mouhotii*, CAS 228365, CAS 228374, CAS 228420, CAS 228444; *muhlenbergii*, LMNH 55352, MCZ 52248; *mutica*, LMNH 54883; *P. nelsoni*, CM 67311; *nigra*, CAS 8125, CAS 8289; *nigrinoda*, TUMNH 15147, TUMNH 15317, TUMNH 15408, TUMNH 15750; *ocellata*, CAS 228336; *G. oculifera*, TUMNH 26, TUMNH 3359, TUMNH 7548, TUMNH 12402, TUMNH 16928; *P. oculifera*, CAS 165598, CAS 220645, CAS 220646; *odoratus*, YPM 13622, CAS 228351, CAS 228352, CAS 228353; *orbicularis*, CAS 173223, CAS 228347, CAS 228415, CAS 228447, LMNH 10347, YPM 15479; *T. ornata*, CAS 228381, CAS 228382, CAS 228383, CAS 228384, TNHC 62532; *ouachitensis*, CM 61656, CM 84696; *pardalis*, CAS 148630, CAS 228349, CAS 228410, CAS 228418, CAS 228432, CAS 228449; *petersi*, CAS 8608, CM 124246, CM 124247; *picta*, CAS 13889, CAS 228379, CAS 228380, CAS 228385; *N. platynota*, CAS 228342, CAS 228450, CM 118586, FMNH 224216, YPM 14678; *polyphemus*, CAS 14090, LMNH 43344, LMNH 43354, LMNH 59320; *pulcherrima*, CAS 11754, CAS 228355, CAS 228366, CAS 228377; *pulchra*, LMNH 48092; *punctularia*, YPM 465, CAS 228348; *reevesii*, CAS 31437, CAS 228361, CAS 228364; *reticularia*, CAS 228338, CAS 228388, LMNH 14565, LMNH 14569, LMNH 49145, LMNH 54856, LMNH 78580; *rubida*, CM 87907, CM 87908; *rubriventris*, CM 34409, CM 45188; *scripta*, CAS SUR8642, CAS 228436, CAS 228442, LMNH 15684; *serpentina*, CAS 228452, YPM 6369, CAS 228457; *siebenrocki*, CAS 228393; *signatus*, CAS 228405, MCZ 42217, MCZ 42218; *sinensis*, CAS 18031, CAS 228339; *spengleri*, CAS 21008, CAS 228331, CAS 228332, CAS 228343, CAS 228371, YPM 11653, YPM 14445; *spinifera*, CAS 65705, CAS 228350, CAS 228354, YPM 656; *spinosa*, CAS 228368, CAS 228459; *subglobosa*, CAS 228334; *subtrijuga*, CAS 16996, CAS 228445, CAS 228446, CAS 228453, CAS 228454; *subrufa*, CAS 228389, CAS 228390, CAS 228391; *tcheponensis*, CAS 228363, CAS 228370; *tecta*, CM 89923; *tentoria*, FMNH Moll3026, FMNH Moll3028, FMNH Moll3032, FMNH 259430; *tentorius*, MCZ 41944, MCZ 46604; *terrapin*, CAS 43640, CAS 228340, CAS 228387, YPM 2983; *texana*, CAS 30965, CAS 228437, CAS 228438, CAS 228439, CAS 228440, CAS 228441, CAS 228456, CAS 228458; *thurjii*, FMNH 224135, FMNH 224153, MCZ 62523, MCZ 62524, YPM 14072, YPM 14073, YPM 14074; *tornieri*, CAS 139704, CAS 228395, CAS 228403, CAS 228417, CAS 228424; *tri-*

fasciata, CAS 228337, MCZ 5218; *trijuga*, CAS 12463, CM 89921, CM 124227, YPM 15453; *versa*, TUMNH 4484, TUMNH 10510, TUMNH 16192; *yuwonoi*, YPM 12626.

Appendix 2

Generic synonymies for all currently recognized testudinoid species and all outgroup species used herein. Synonymies are based only on common usage during the last 50 years.

Ingroup

adiutrix	*Chrysemys, Pseudemys, Trachemys*
agassizii	*Gopherus, Xerobates*
alabamensis	*Chrysemys, Pseudemys*
amboinensis	*Cuora*
angulata	*Chersina, Goniochersus, Neotestudo, Testudo*
annamensis	*Annamemys, Mauremys*
annandalii	*Hieremys*
annulata	*Callopsis, Geoemyda, Nicoria, Rhinoclemmys*
arachnoides	*Pyxis*
areolata	*Callopsis, Geoemyda, Nicoria, Rhinoclemmys*
areolatus	*Homopus*
aurocapitata	*Cuora*
barbouri	*Graptemys, Malaclemys*
baska	*Batagur*
bealei	*Clemmys, Sacalia*
belliana	*Kinixys*
berlandieri	*Gopherus*
blandingii	*Emydoidea, Emys, Neoemys*
borneensis	*Orlitia*
borneoensis	*Callagur*
boulengeri	*Homopus*
caglei	*Graptemys*
callirostris	*Chrysemys, Pseudemys, Trachemys*
carbonaria	*Chelonoidis, Geochelone*
carolina	*Terrapene*
caspica	*Clemmys, Mauremys*
chilensis	*Chelonoidis, Geochelone*
coahuila	*Terrapene*
concinna	*Chrysemys, Pseudemys*
crassicollis	*Siebenrockiella*
decorata	*Chrysemys, Pseudemys, Trachemys*
decussata	*Chrysemys, Pseudemys, Trachemys*
dentata	*Cyclemys, Geoemyda*
denticulata	*Chelonoidis, Geochelone*
depressa	*Geoemyda, Heosemys*
dhongoka	*Kachuga*
diademata	*Geoemyda, Rhinoclemmys*
dorbigni	*Chrysemys, Pseudemys, Trachemys*
dussumieri	*Aldabrachelys, Dipsochelys, Geochelone, Megalochelys*
elegans	*Geochelone*
elongata	*Geochelone, Indotestudo*
emolli	*Chrysemys, Pseudemys, Trachemys*
emys	*Geochelone, Manouria*
ernsti	*Graptemys*
erosa	*Kinixys*
femoralis	*Homopus*
flavimaculata	*Graptemys, Malaclemys*
flavomarginata	*Cistoclemmys, Cuora, Geoemyda*
flavomarginatus	*Gopherus*
floridana	*Chrysemys, Pseudemys*
forsteni	*Geochelone, Indotestudo, Manouria*
funerea	*Callopsis, Geoemyda, Rhinoclemmys*
gaigeae	*Chrysemys, Pseudemys, Trachemys*
galbinifrons	*Cistoclemmys, Cuora*
geographica	*Graptemys, Malaclemys*
geometricus	*Psammobates*
gibbonsi	*Graptemys*
graeca	*Testudo*
grandis	*Geoemyda, Heosemys*
guttata	*Clemmys*
hamiltonii	*Geoclemys*
hermanni	*Testudo*
homeana	*Kinixys*
horsfieldi	*Agrionemys, Testudo*
impressa	*Geochelone, Manouria*
G. insculpta	*Calemys, Clemmys, Glyptemys*
japonica	*Clemmys, Mauremys*
kachuga	*Kachuga*
kleinmanni	*Pseudotestudo, Testudo*
kohnii	*Graptemys*
leprosa	*Clemmys, Mauremys*
leytensis	*Geoemyda, Heosemys*
lobatsiana	*Kinixys*
marginata	*Testudo*
marmorata	*Clemmys, Emys*
melanosterna	*Geoemyda, Rhinoclemmys*
mouhotii	*Cuora, Cyclemys, Geoemyda, Pyxidea*
muhlenbergii	*Calemys, Clemmys, Glyptemys*
mutica	*Clemmys, Mauremys*
nasuta	*Callopsis, Geoemyda, Rhinoclemmys*
natalensis	*Kinixys*
nebulosa	*Chrysemys, Pseudemys, Trachemys*
P. nelsoni	*Chrysemys, Pseudemys*
T. nelsoni	*Terrapene*
nigra	*Chelonoidis, Geochelone*
nigricans	*Chinemys*
nigrinoda	*Graptemys, Malaclemys*
ocellata	*Morenia*
G. oculifera	*Graptemys, Malaclemys*
P. oculifera	*Psammobates*
oldhamii	*Cyclemys*

orbicularis	*Emys*
T. ornata	*Terrapene*
P. ornata	*Chrysemys, Pseudemys, Trachemys*
ouachitensis	*Graptemys*
pani	*Cuora*
pardalis	*Geochelone*
petersi	*Morenia*
picta	*Chrysemys*
planicauda	*Acinixys, Pyxis*
G. platynota	*Geochelone*
N. platynota	*Notochelys*
polyphemus	*Gopherus, Xerobates*
pseudogeographica	*Graptemys, Malaclemys*
pulcherrima	*Callopsis, Geoemyda, Rhinoclemmys*
pulchra	*Graptemys, Malaclemys*
pulchristriata	*Cyclemys*
punctularia	*Geoemyda, Rhinoclemmys*
quadriocellata	*Clemmys, Sacalia*
radiata	*Asterochelys, Geochelone*
reevesii	*Chinemys*
reticularia	*Deirochelys*
rubida	*Callopsis, Geoemyda, Nicoria, Rhinoclemmys*
rubriventris	*Chrysemys, Pseudemys*
scripta	*Chrysemys, Pseudemys, Trachemys*
signatus	*Homopus*
silvatica	*Geoemyda, Heosemys*
sinensis	*Ocadia*
smithii	*Kachuga, Pangshura*
spekii	*Kinixys*
spengleri	*Geoemyda*
spinosa	*Geoemyda, Heosemys*
stejnegeri	*Chrysemys, Pseudemys, Trachemys*
subtrijuga	*Malayemys*
sulcata	*Geochelone*
sylhetensis	*Kachuga, Pangshura*
taylori	*Chrysemys, Pseudemys, Trachemys*
tcheponensis	*Cyclemys, Geoemyda*
tecta	*Kachuga, Pangshura*
tentoria	*Kachuga, Pangshura*
tentorius	*Psammobates*
terrapen	*Chrysemys, Pseudemys, Trachemys*
terrapin	*Malaclemys*
texana	*Chrysemys, Pseudemys*
thurjii	*Hardella*
tornieri	*Malacochersus*
travancorica	*Geochelone, Indotestudo*
tricarinata	*Geoemyda, Melanochelys*
trifasciata	*Cistoclemmys, Cuora*
trijuga	*Geoemyda, Melanochelys*
trivittata	*Kachuga*
venusta	*Chrysemys, Pseudemys, Trachemys*
versa	*Graptemys, Malaclemys*
werneri	*Testudo*
yaquia	*Chrysemys, Pseudemys, Trachemys*
yniphora	*Asterochelys, Geochelone*
yunnanensis	*Cuora*
yuwonoi	*Geoemyda, Leucocephalon, Notochelys*
zhoui	*Cuora*

Outgroup

caretta	*Caretta*
dumerilianus	*Peltocephalus, Podocnemis*
C. insculpta	*Carettochelys*
fimbriatus	*Chelus*
gibba	*Phrynops, Mesoclemmys*
madagascariensis	*Erymnochelys, Podocnemis*
megacephalum	*Platysternon*
odoratus	*Kinosternon, Sternotherus, Sternothaerus*
scorpioides	*Kinosternon*
serpentina	*Chelydra*
siebenrocki	*Chelodina, Macrochelodina*
spiniferaApalone, Trionyx	
subglobosa	*Emydura, Tropicochelymys*
subrufa	*Pelomedusa*
temminckii	*Macroclemys, Macrochelys*

Appendix 3

Distribution of character states for 70 characters among 46 species of testudinoid turtles; a = 0/1; b = 0/2; c = 0/3; d = 0/1/2; e = 1/2; f = 1/3; g = 2/3.

agassizii					
11a10	00000	000?0	11010	00110	00001
01000	03200	00000	00120	22001	22200
00000	10110				
amboinensis					
00a00	00010	00001	00000	00010	00000
00000	01110	00200	0a011	11110	00001
20000	00000				
annandalei					
0010?	00020	00011	10001	00010	00000
00100	01100	00000	00a10	34000	00001
00000	0000?				
annulata					
00a00	00010	0010a	00000	00010	00000
00000	03100	00000	000?0	11000	0??01
00000	00010				
barbouri					
00001	11000	01010	10000	10000	101a0
00001	10000	00000	00000	34000	22200
00000	00001				
baska					
00001	00000	00010	10001	00000	00a02
11100	00010	00000	10110	43000	00000

00000 01000
bealei
00000 00010 00000 10000 00010 00000
00000 00000 0??00 0a010 34000 0000?
00000 00000
blandingii
00000 00000 000?0 00000 10000 00000
00000 0c000 00000 01001 11110 1120a
10011 00000
borneensis
00100 00000 00010 00000 00010 10000
00000 00000 00010 00a10 33000 00000
00000 00000
borneoensis
00001 00000 00010 10001 00010 00001
11100 00000 00100 00a10 43000 00000
00000 00000
carbonaria
11010 00000 000?a 11000 00111 00001
00000 01201 00000 00120 22001 22210
00000 10110
caspica
00000 00010 0000a 00000 00010 00000
00000 00000 00000 0aa10 34000 00001
00000 00000
crassicollis
00a00 00000 00000 10000 00010 10000
00001 00000 00010 00a10 33000 00001
00000 00000
elongata
11010 00000 000?a 11000 00111 00001
00000 03200 00000 00020 22001 ???11
00000 10110
dentata
00000 00010 00000 00000 00000 00000
00001 01100 00001 00011 11000 01101
00100 00000
emys
11010 00000 000?a 11000 00110 00001
00000 01000 02000 00aa0 22001 ???00
00000 10110
flavomarginata
00010 00020 0000a 00000 00010 00000
00000 01110 00100 00011 11110 ?1101
21000 00010
graeca
11010 00000 000?1 11000 10111 00001
00000 03200 00000 00a20 22000 22211
00000 10110
grandis
0010a 00020 00000 00000 000a0 00000
00001 01100 0000a 00a10 34000 00001
00100 00010
guttata
00010 00000 00000 00000 10000 00000
00000 00000 00000 00000 34000 10201
00000 00000
hamiltonii
01101 00001 00000 10000 00010 00110
00111 00000 00000 00a10 33001 0000a
00000 00000
homeana
11010 00000 000?1 11000 00111 00000
00001 0110a 00000 00020 22001 ???1a
20000 10110
horsfieldi
11010 00000 000?0 11000 a0111 00001
00000 03200 00000 00020 22000 ???11
00000 11110
kachuga
00101 00000 00010 10001 00010 10001
11100 00000 01000 10110 43000 00000
00000 0000?
mouhotii
00010 00010 00000 11100 00010 00000
00011 01100 00000 00011 11110 00001
a0000 00010
P. oculifera
11010 00000 000?? 11000 00111 00001
00001 01200 00000 00120 22001 ???10
00000 10110
orbicularis
00000 00000 00000 00000 a0000 00000
00000 00000 00000 0a001 11010 1120a
10010 00000
T. ornata
00010 00010 00000 00000 10000 00000
00000 00010 00200 00001 00110 ed201
20011 00010
pardalis
11010 00000 000?a 11000 00111 00001
00000 0f201 00000 00120 22001 ???10
00000 10110
petersi
01100 00000 00010 10001 00010 01111
12100 02000 00100 00110 34000 00000
00000 00001
picta
00001 10000 00010 00000 10000 00000
00000 00000 00000 0a0a0 34000 2220a
00000 0000a
N. platynota
01101 00010 00000 00000 00a10 00000
00001 00000 10100 00001 03010 00101

10000 00000 00000 10110

polyphemus

11010 00000 000?0 11000 a0110 00001
01000 0a200 00000 00120 22001 22200
00000 10110

pulcherrima

00a00 00010 00001 00000 a0010 00000
00000 01100 00000 000a0 14000 01?01
00000 00000

reevesii

00101 10000 00000 10000 00010 10110
00110 00000 00000 00aa0 33000 00001
00000 00000

reticularia

00000 10000 000?0 00000 10000 00000
00000 00000 00000 010a0 34000 22200
10000 00001

scripta

00001 10000 00010 10000 10000 00101
10000 00000 00000 00000 34000 22200
00000 0000a

sinensis

00001 00000 00010 10001 10010 00001
00000 00000 00000 00aa0 33000 00001
00000 00000

spengleri

000a0 00000 00100 10100 00010 00000
00011 01100 00000 00000 34000 00001
00000 00010

subtrijuga

00100 01100 11000 10000 01010 10100
00110 00g00 00000 00a10 33000 00000
00000 00000

tentoria

00001 00000 00010 10001 00010 10001
10100 10000 01000 10110 43000 00000
00000 0000?

terrapin

00001 10000 00010 10000 a0000 10100
00000 00000 00000 0a000 34000 ed200
00000 00001

texana

00001 10000 0a010 10000 a0000 00101
10000 00000 00000 00000 34000 22200
00000 0000a

thurjii

00001 00000 00010 10001 00000 01011
11100 00000 00100 00110 43000 00000
00000 00001

tornieri

11010 00000 000?1 11000 00111 00001
00000 0??00 00000 00020 22000 2220a

Trade Data and Some Comments On the Distribution of *Mauremys annamensis* (Siebenrock, 1903)

MINH LE[1,*], THANG HOANG[2], AND DUC LE[3]

[1]*American Museum of Natural History, Department of Herpetology, Central Park West at 79th Street New York, NY 10024*

[2]*19th Le Thanh Tong St., Hanoi, Vietnam*

[3]*WWF Indochina Programme, 53-Tran Phu St., Ba Dinh, Hanoi, Vietnam; IPO Box 151, Hanoi, Vietnam*

** E-mail: minhl@amnh.org*

Abstract. - This trade survey of Annam Pond Turtle reveals that this species is likely to have larger distribution than previously thought. The records in the trade in Quy Nhon and Ho Chi Minh City suggest its range could extend much further south. In addition, given the one way south-north trade route, the absence of *Mauremys mutica* in the trade south of Hai Van Pass and the reported absence of *M. annamensis* in the trade north of the Pass support the hypothesis that the Pass is the natural barrier for the two species ranges. This hypothesis combined with the long existence of the Pass might indicate that the speciation between the two species happened when their ancestors dispersed across the Pass, and were subsequently isolated, by the means of rafting or walking through narrow land strip emerged during the low sea level period. In terms of conservation, *M. annamensis* has become much rarer even in the trade, suggesting immediate conservation measures to protect it.

Key words. - *Mauremys annamensis*, Bataguridae, Hai Van Pass, Truong Son Range, distribution, biogeography.

Distribution of *Mauremys annamensis*. - The Annam Pond Turtle, *Mauremys annamensis*, was first described by Siebenrock in 1903 based on a specimen collected from Phuc Son or Phuoc Son (15° 33' 00" N; 108° 04' 00" E) (southwest of Tourane, now known as the city of Da Nang) in Central Vietnam. Another specimen was collected by Bourret from Fai Fo (Hoi An), an ancient city about 50 km from Da Nang (Bourret, 1941). Since then, it seems that little effort has been made to record the distribution of this species in the wild. Iverson (1992) and Iverson *et al.* (1999) cite only the above records from Bourret for their maps of global turtle distribution.

According to Bourret (1941), this species was very abundant in the marshes and slow-moving water bodies in the lowland areas of the cities of Hoi An and Da Nang. Both Hoi An and Da Nang, however, are now very populated cities surrounded by rice paddies, which are unlikely to be suitable habitats for this species. This is because the intensive use of chemicals, such as herbicides and pesticides, in rice paddies through out Vietnam makes it difficult for turtles to survive in this environment.

To better understand its distribution, we did a 6-day trade survey in the August of 1996. The survey covered three cities, namely Quy Nhon (13° 46' 00" N; 109° 14' 00" E), Da Nang, and Hue (16° 28' 00" N; 107° 36' 00" E), and their surrounding areas. We interviewed turtle dealers at the collecting points, where turtles were bought from collectors and awaited to be shifted to China. We used the book Turtles of the World (Ernst and Barbour, 1989) for identification key. In addition, since the initial purpose of the survey is to determine the trade status of *M. annamensis*, we identified, but did not record the availability of other turtle species in the collecting points.

We observed that this species was still common in the trade in Quy Nhon and Da Nang. In Quy Nhon and its outskirt, we visited three collecting points. In the first one, we identified 2 adult *M. annamensis*. In the other two collecting points, we found 3 and 4 juveniles, respectively. In Da Nang and its surrounding areas, we visited four sites with three to four specimens in each sites. They were all young and juvenile turtles. From the interviews with local people in Quy Nhon and Da Nang, it was apparent that this species could well survive in the human-modified environment, such as lakes and fishponds, if there were no collecting activities by local people. Local trade dealers and collectors, encountered in collecting points in Quy Nhon and Da Nang, suggested that this species still existed in the water bodies in the nearby region. Le and Trinh (2001) also indicated that the species could occur in Tra My, Tien Phuoc, and probably Hiep Duc Districts, Quang Nam Province.

The occurrence of *M. annamensis* in Quy Nhon is very interesting since this species had been believed to have very restricted distribution. More remarkably, Le and Broad (1995) reported that *M. annamensis* even extended far south to Ca Mau, Minh Hai Province inhabiting *Melaleuca* forests (around 9° 29' 00" N; 105° 20'

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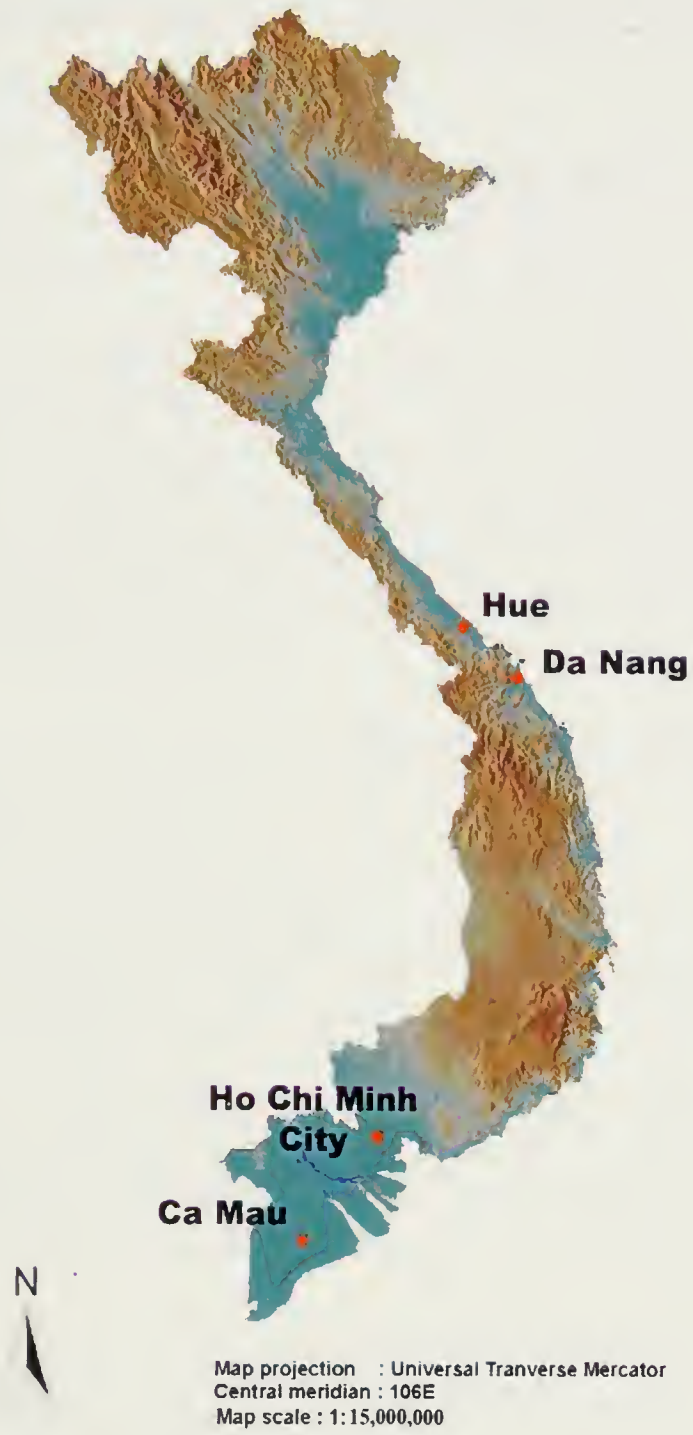

Figure 1. Topographic map of Vietnam.

00" E;) situated at the southern tip of Vietnam. It is possible that Le and Broad misidentified this species in their survey (Jenkins, 1995). However, Peter Paul van Dijk, Le Trong Dat, and Douglas Hendrie on May 30, 2000 found this species in Ben Chuong Duong Street shops in Ho Chi Minh City (Hendrie, 2000a). This evidence combined with the one-way trafficking of turtles (from south to north) (Le and Broad, 1995) indicates that *M. annamensis* may have much wider distribution than previously thought.

This hypothesis is also supported by Le and Trinh (2001). Their interviews with local dealers, in May 2001, in Quang Nam Province revealed that one dealer in Thang Binh District bought this species from the shipments transported from the south. Le and Trinh (2001) also suggested that *M. annamensis* is naturally distributed in Tra My, Tien Phuoc, and probably Hiep Duc Districts, Quang Nam Province. These authors also indicated an interesting fact that turtle hunters only sell their animals to the local dealers. This manner of trade demonstrates that the local trade data can be informative in determining the limit of the natural ranges of some species.

It is noted that we did not encounter any *M. mutica* in the areas in Quy Nhon and Da Nang. Le and Trinh (2001) also did not find any *M. mutica* in their trade investigation, which covered seven districts and one town in Quang Nam Province, and the city of Da Nang. According the pattern of turtle trade in Vietnam plotted by Le and Broad (1995), turtles have been collected from the south and transported to the north. They are finally destined in the border between and Vietnam and China, where they are traded in an enormous volume. The one-way south north trafficking leads to the conclusion that *M. mutica* does not occur in Da Nang, located in the southern side of Hai Van Pass, or southern areas of the city.

In the survey, we found no evidence for *M. annamensis* distributed in the northern side of the Hai Van Pass. Interviews with turtle dealers from two collecting points in the city of Hue (north of Hai Van Pass) revealed that this species was only transported to the city from the south and there was no record of this species in the surrounding areas. It is also interesting that the dealers called this species Rua Dep Nam (Beautiful Southern Turtle) as compared to Rua Dep Bac (Beautiful Northern Turtle), here referred to *Maurenys mutica*. According to them, *M. mutica* came only from areas north of Hai Van Pass. In the house of a trader in Hue, we observed about 20 *M. mutica* from 1 to 2 kg, but no *M. annamensis*. In the other site, we did not find any *M. mutica* or *M. annamensis*.

Given the fact that Hue and Da Nang is only 100 km apart, it is very likely that Hai Van Pass (at around 16°N) forms the natural boundary of these two species since the Pass stands in between two cities. Records from previous studies also support this hypothesis (Iverson, 1992; Nguyen and Ho, 1996). Thus, the mountain range, which cuts through the country, is most certainly the northern boundary of *M. annamensis*' range and southern boundary of *M. mutica*'s range. Because they are the lowland inhabitants, the Pass (1712m above sea level at the summit) seems to be a significant barrier.

Some studies have suggested that the Pass is the border between two zoological regions, Northern Central Vietnam (Northern Truong Son) and Central Vietnam (Central Truong Son) for such groups as rodent, bird, fish, and lizard (Bobrov, 1993; Dao, 1978, Cao, 1989). In addition, Fooden (1996) showed in Fig1i that the distribution two closely related gibbon taxa, *Hylobates gabriellae siki* and *H. gabriellae gabriellae*, has been separated by the Pass. Even though primate is more likely to possess higher dispersal ability, the barrier seems significant enough to block their expansion. In

fact, the Truong Son Mountain Range in general has established dispersal barriers for *Cuora galbinifrons* species complex (Stuart and Parham, 2004).

Hai Van Pass is a part of Truong Son Mountain Range (Annamite Mountains), which runs throughout most of the country's length. The Pass meets the South China Sea and effectively divides the country into two different sections. It is formed by aluminous granite, and probably emerged about 250 Mya in the early Triassic (Lepvrier *et al.*, 1997). If the Pass is actually the natural boundary of these two species' ranges, it can be hypothesized that the speciation between *M. annamensis* and *M. mutica* was occurred when their ancestors dispersed across the Hai Van Pass and then were subsequently isolated. Since these turtles are good swimmers, one possible scenario is that they rafted on the sea to get to the other side of the Pass. Another possibility is that they traveled south through a narrow land belt exposed during the low sea level period. According to Prentice and Denton (1988), before from 6 Mya to 0.9 Mya the sea level fluctuated at an average of 70m below the present sea level. At this level, a few kilometers of the continental shelf could be opened to the east of the Pass (Voris, 2000) and well served as a travel route for these turtles. However, these hypotheses are very preliminary and, therefore, should be carefully tested in a much more comprehensive study in the future.

Trend in the trade of *M. annamensis*. - In recent years, turtles in the Southeast Asian region, especially in Vietnam, have been critically threatened by the trade with China. The trade has been driven by the Chinese long tradition of using turtles as food and medicines. Many species might go extinct in very near future unless urgent protection measures are implemented (van Dijk, 2000; Hendrie, 2000). In Vietnam, species such as *Cuora trifasciata*, believed to be able to cure cancer, is at considerable risk due to its significant economic value (about 1000 USD per individual or even more (Lovich *et al.*, 2000; Le and Trinh, 2001)). For *M. annamensis*, in addition to the general demand from China, there are also interests in keeping them as pets in countries such as the U.S. The United States Fish and Wildlife Service indicated that from 1996 to 1999 small numbers were imported to the U.S. from Vietnam (Consideration of Proposals for Amendment of Appendices I and II). Weissgold (2002) even maintained that the imports increased during 1999-2001. Due to the risk posed by the trade and habitat destruction, this species has been listed in the Appendix II and in the critically endangered category by CITES and IUCN, respectively.

It is clear that the number of *M. annamensis* has declined dramatically in recent years. The market value of this species, approximately $5 to $7 per kg (Le and Broad, 1995; Le and Trinh, 2001; and this survey), can generate substantial interests among poor local people. In our survey in 1996, this species was still pretty common in the trade. My personal observation in Dong Xuan market, Hanoi, in 1998 also confirmed the commonness of this species. More recently, Hendrie (2000b) reported that the occurrence of this species in turtle confiscated shipments is less frequent compared to the previous years. Le and Trinh (2001) reported that this species was very rare in the trade compared to other species – only second to Golden Turtle (*Cuora trifasciata*). In fact, they only encountered only one juvenile in the whole period of the survey. Thus, this species should be given the highest priority in conservation programs in the near future.

Acknowledgments

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Neotype of *Testudo terrestris* Forsskål, 1775 (Testudines, Testudinidae)

JARMO PERÄLÄ[1] AND ROGER BOUR[2]

[1]*Department of Biological and Environmental Sciences, PO Box 65 (Biocenter 3, Viikinkaari 1), FIN-00014 University of Helsinki, Finland; E-mail: jarmo.perala@helsinki.fi*

[2]*Laboratoire des Reptiles et Amphibiens, Muséum national d'Histoire naturelle, 25 rue Cuvier, 75005 Paris, France; E-mail: bour@mnhn.fr*

Abstract. - We discuss and clarify the nomenclatural status of *Testudo terrestris* Forsskål, 1775. *Testudo terrestris*, a taxon based on a syntype series, was until now a valid name for tortoises from parts of Egypt, Arabia and the Levant, according to the International Code of Zoological Nomenclature. On the contrary, all type locality restrictions from the 20th century regarding the name *Testudo terrestris* Forsskål, done without the fixation of a name-bearing specimen (lectotype or neotype), are invalid. Because the name is valid, and because the syntypes, listed but not identified in the original description, are untraceable, and to permanently fix the name and its type locality, we designate a neotype for *Testudo terrestris* Forsskål based on a specimen from Aleppo, Syria.

Key words. - Taxonomy, Testudines, Testudinidae, *Testudo terrestris* Forsskål, 1775, nomenclatural validity, neotype.

Forsskål and Mediterranean tortoises. - During his fatal travel (1761-1763) in the eastern Mediterranean countries, the Finn Petter Forsskål (1732-1763) encountered tortoises, briefly described by the name *Testudo terrestris* in his diary, which was published as a posthumous work by Carsten Niebuhr (1733-1815), a German traveller and surveyor, in 1775 [= Forsskål, 1775]. Strauch (1862: 69) remarks in a footnote that Forsskål (1775) discusses a tortoise, *Testudo terrestris*, which occurs in Aleppo and Lebanon, without describing it, and Anderson (1896: 68) writes that "it is useless attempting to identify this animal" "from Loheia, north of Hodeida," with reference to Forsskål (1775). Forsskål's itinerary took him through the following localities: Malta, Smyrna (Izmir), Constantinople, Alexandria, Rosetta, Cairo, Suez, Jedda, ending up in Yarim, Arabia Felix (Yemen), where Forsskål died of malaria in 1763. Tortoises were reported from Al Luḩayyah (Yemen), Cairo (Egypt), Lebanon, Lattakia (Al Lādhiq - īyah) and Aleppo (both in Syria) (Fig. 1). Forsskål (1775) indicated that the chelonians are called "Zolhafae" by the Arabs (Forsskål, 1775); as for their distribution, he specified: "Kahirae non frequens vivit, Aleppo autem & ad Libanon copiosor," translated by Daudin (1801: 225) as: "It is rare in Cairo, but can be found rather abundantly near Aleppo and towards Mount Lebanon". At best, Forsskål himself was thus able to see tortoises *in situ* in northern Egypt (Nile Delta and Suez area) only, that is those which are actually called either *Testudo kleinmanni* Lortet, 1883 (the Egyptian tortoise) or the vicariant *T. werneri* Perälä, 2001. This interpretation is in accordance with the vernacular name of the Egyptian tortoise, *fide* Anderson (1898: 30; "Sohlafa" pronounced "Zihlifa") and Flower (1933: 742; "Educated people in Egypt employ the word 'Zalheefah'"). Niebuhr's subsequent route back home took him via Basra, Baghdad, Mosul, Diyarbakır, Aleppo, Lebanon and Palestine (Hansen, 1962; Niebuhr, 1772, 1973). Niebuhr, the only surviving member on the expedition to Arabia Felix, continued to Bombay (Mumbai), India, from where he shipped the natural history notes (Niebuhr, 1772: xix) and specimens (Niebuhr, 1973: 120) collected by Forsskål via London to Copenhagen. A considerable amount of material in the Forsskål collection in Copenhagen was destroyed in bombings by the British in 1807 (Nielsen, 1993). The type of *T. terrestris* is said to be "apparently lost" (Webb in Iverson, 1992). The name is not fixed to a single name-bearing specimen.

Nomenclatural validity of *Testudo terrestris*. - *Testudo terrestris* Forsskål, 1775, one of the oldest species group names in the genus *Testudo* Linnaeus, 1758 *sensu lato* (in the sense of Lapparent de Broin, 2001; Perälä 2002a), is nomenclaturally valid, according to the present International Code of Zoological Nomenclature (ICZN, 1999): it was published before 1931 and thus does not need to have a full diagnosis by which it can be identified. Only "a description or a definition" *per se* is needed (ICZN, 1999: Article 12). In this respect the remark by Forsskål (1775) pertaining to the tortoises' length ("...foot-long..."), as well as that made of the shapes of plastra of both sexes, is enough, even if these characters were incorrect. Moreover, although the name

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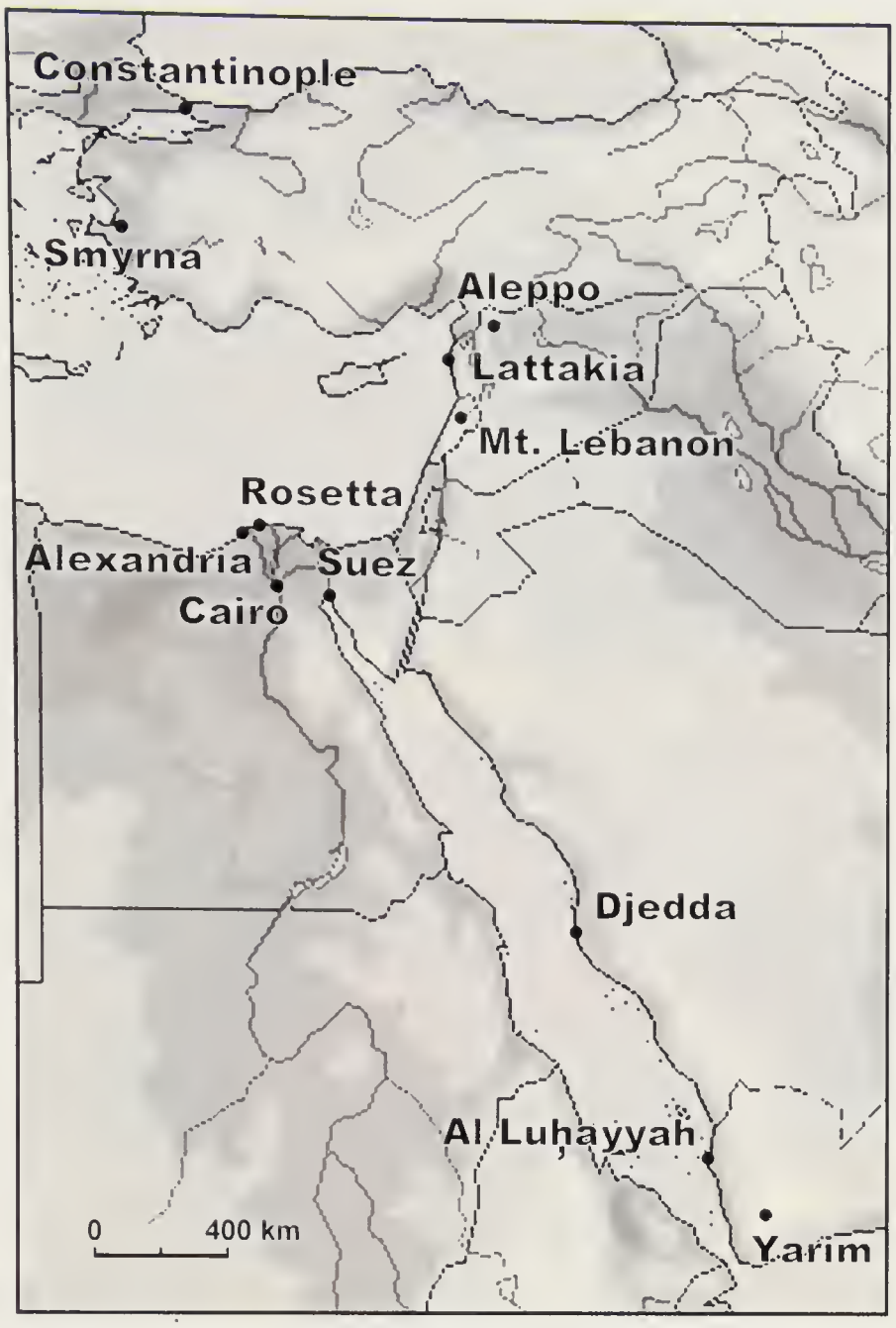

Figure 1. Map of geographical localities mentioned in Forsskål's (1775) description, which together constituted the type locality of *Testudo terrestris* Forsskål until the present work.

is accompanied by the remark "Obs." (Forsskål, 1775: 12), it is also listed under the headings "Descripta" (p. viii) as well as "Nominata" (p. ix) alongside with valid names such as *Testudo triunguis* Forsskål, 1775, that is, current *Trionyx triunguis*. The book contains a multitude of other descriptions of valid taxa which cannot be rejected based on the arguments (see below) about the use of the Latin language, a contemporary standard, alone. Based on Niebuhr's subsequent route back home, Gasperetti et al. (1993) suggested that it may actually be Niebuhr who is responsible for the name *T. terrestris* Forsskål. As Niebuhr's role is not explicit in the original publication, the authorship of the name remains with Forsskål (ICZN, 1999: Art. 50.1.1).

***Testudo terrestris* overlooked, rejected, then revalidated**. - After its publication, and during about 180 years, the nominal species *Testudo terrestris* Forsskål, 1775, although nomenclaturally valid, was nevertheless overlooked by most authors (except Strauch, 1862 and Anderson, 1896), some of them (Gray, 1831; Duméril and Bibron, 1835) only mentioning *Testudo zolkafa* and *Testudo zohalfa*, respectively, based on Forsskål's (1775) vernacular Zolhafae, and which nomina nuda appear in the above works as synonyms of *Testudo graeca* Linnaeus, 1758 and *Testudo mauritanica* Duméril and Bibron, 1835, respectively. On the other hand, at least one scientist worked to revive the nominal species. A brief history of the case is presented by Bour in David (1994: 86). The name *Testudo terrestris* Forsskål was resurrected, and therefore revalidated, by Wermuth (1956: 402), who improperly (without specimen fixation) designated "Arabia" as type locality. Simultaneously, Wermuth considered to ask the International Commission on Zoological Nomenclature to invalidate the nominal species *Testudo terrestris* Forsskål; unfortunately, his attitude changed radically (1958: 149-153) and he used this name to designate the Near Eastern population of *Testudo* (as *Testudo graeca terrestris* Forsskål), restricting the type locality to "Libanon-Gebirge, Israel" [sic], and mistakenly extending its range to Libya. It must be outlined that there is a gap in the range of *Testudo graeca* (*sensu lato*) complex tortoises between Israel and Libya, the latter containing the range of the recently described species *Testudo cyrenaica* Pieh & Perälä, 2002. Wermuth had at his disposal one Libyan specimen (SMF 36127; paratype of *T. cyrenaica*), from Dernah, which he thought to be identical with Middle-Eastern tortoises (Pieh & Perälä, 2002). Wermuth's validation was disapproved by Buskirk (in Ernst et al., 2000; unpublished manuscript from the early 1990s; and pers. comm. to both authors); Highfield (in Ernst et al., 2000; and: http: //www.tortoisetrust.org/articles/newfloweri.html); J. F. Parham (pers. comm.); and Perälä (1996); among others. Their opposition is based on several arguments such as: a description is lacking with reference to the remark "Obs." in Forsskål (1775); the species cannot be identified from the "description"; there is no type specimen; a "false" type locality; the name "*Testudo terrestris*" is just Latin for a terrestrial chelonian, used without intention to describe a new species.

Need of a neotype. - Rather to resurrect *Testudo terrestris* Forsskål (Wermuth, 1956), it would have been preferable: (1) either to suppress this imprecise name (and which is a more recent homonym of the nominal species *Testudo terrestris* Fermin, 1765, for which Wermuth had to successfully request the invalidation by the International Commission on Zoological Nomenclature; ICZN, 1963: Opinion 660); (2) either to use it to name *Testudo kleinmanni*, a name revalidated only in the 1950s by Mertens & Wermuth (1955), and independently by Loveridge & Williams (1957). It could still be possible to ask the ICZN to officially suppress the name *Testudo*

Figure 2. Neotype of *Testudo terrestris* Forsskål, 1775, specimen n° NMW 18674: 2, sub-adult female. Upper left: lateral view (right side); Upper right: dorsal view; Lower left: ventral view. Lower right: living specimen of *Testudo terrestris*, adult female, from Aleppo (topotype); CL = 185 mm, MI = 143 mm, HE = 99 mm.

terrestris Forsskål, 1775. However, we reject this option because: (1) the name is presently widely used (in all recent check-lists, with more than fifty references), although with vagueness about the identity of the concerned population; (2) there is no valid name to designate the species of *Testudo* living in the Middle-East, more precisely in the area of the upper Euphrates - Tigris drainage; (3) the name *Testudo terrestris* Forsskål, 1775 became available by the very ruling of the International Commission on Zoological Nomenclature (ICZN, 1963), and it is unlikely that the Commission would reverse its opinion. Accepting the nomenclature proposed by Wermuth, one of us (RB) proposed to emend the type locality of *Testudo terrestris* Forsskål to the vicinity of Aleppo (= Halab), Syria (Bour, 1989: 14), in the interest of clarifying the status of this taxon and as a first step towards the description of a neotype. However, such restriction of the type locality, as well as the earlier restrictions proposed by Wermuth (1956, 1958), are invalid according to the Code (ICZN, 1999; Art. 76.3), because these actions were not done in connection with the selection of a lectotype or neotype. Therefore we here propose the formal description of a neotype of *Testudo terrestris* Forsskål, 1775. All the animals listed (although not identified; therefore untraceable) by Forsskål (from Al-Luḫayyah, Cairo, Lebanon, Lattakia and Aleppo) actually represent syntypes, according to the Code (ICZN, 1999; Art. 72.1.1), and thus the type locality of *T. terrestris* encompasses the region containing all those localities (ICZN, 1999; Art. 73.2.3). A neotype could legitimately be selected from any of those *per se*. Besides sea turtles, only *Centrochelys sulcata* (Miller, 1779), a land tortoise (possibly introduced), and *Pelomedusa subrufa* (Lacepède, 1788), a fresh-water turtle, are known to occur in Yemen (Obst & Wranik, 1987; Gasperetti et al., 1993; Al Safadi, 1997); therefore no *Testudo* sp. could have been observed in Al-Luḫayyah by the Forsskål - Niebuhr expedition. Following the earlier choice, made in accordance with the available data, and also with the current taxonomical practice (e.g., Perälä, 2002b), in order to preserve the stability of the nomenclature, and

to objectively delimit *Testudo terrestris* Forsskål from all other species in the *Testudo graeca* (*s.l.*) complex, we choose a specimen collected in Aleppo (and which locality has by chance a historical background in tortoise literature: cf. Siebenrock, 1913).

The neotype of *Testudo terrestris*. - To fix the name and type locality, we hereby designate a specimen from the Vienna Natural History Museum No. NMW 18674:2, collected in Aleppo by Viktor Pietschmann in March 1910, as the neotype of *Testudo terrestris* Forsskål, 1775, according to Articles 75 and 76 (ICZN, 1999). The neotype is a subadult female with a straight-line carapace length (CL) of 136.8 millimeters. Note: all morphometric characters are according to the standards published in Perälä (2001). As a result of our neotype designation (ICZN, 1999; Art. 76.3), the type locality of *Testudo terrestris* Forsskål, 1775 is restricted to Aleppo (Alep, Halab; 36°12' N, 37°09' E), Syria (Syrian Arab Republic). (For the range of *T. terrestris*, see Perälä, 2002b.)

Description. – Sub-adult female. Most scutes marked with about a dozen of conspicuous growth ridges and grooves; areolae of the carapace feebly bumped, neatly displaced caudally, and also dorsally on the costals. Longitudinal profile high, regularly domed, highest at third vertebral, slightly behind the middle of the shell (Fig. 2, top left). The outline of the shell short, squarish, anterior and posterior free borders only very feebly cut out. Vertebrals wide in dorsal view, the fourth the smallest; the first one with almost straight lateral borders, moderately wider anteriorly than posteriorly (Fig. 2, top right). Cervical (= nuchal) four-sided, very wide; supracaudal distally as wide as vertebrals, regularly convex in its middle; all common sutures of marginals nearly sub equal (= height of lateral ones, and length of anterior and posterior ones); only marginals 9-11 are slightly flaring. Gulars well prominent but short and narrow, their common suture very short; a pair of rather large axillaries on each side; pectorals with a very short common (medial) suture, included about four times in the medial suture of humerals; inguinals small, separated in a larger distal part and a very small proximal part contacting femorals; rear lobe of plastron hardly mobile, short, anals both long and wide, with parallel anterior and posterior borders: their particular shape at first sight resembles the usual shape observed in males (Fig. 2, bottom left). Head covered above with two large and roughly pentagonal scutes, the frontal and the prefrontal, symmetrical about their common suture. Five nails at each hand, the inner one smaller but well developed; four at each foot. Anterior side of the fore-arm covered between the elbow and the wrist by about fifteen large scutes, the four largest being triangular, neatly distinct from the background of the scaly skin; outer border of this area covered by a row of six triangular, overlapping scutes. Tail relatively long and regularly tapering, also giving a rather masculine appearance, ending with slightly enlarged but discrete flat scutes; a small isolated spur on each thigh.

General color greenish yellow, often lighter close to the sutures, with large darker, grayish areas apparently deep in the scutes. Blackish marks reduced on the carapace, limited to incomplete and irregular narrow lines along the anterior sutures of the scutes (marginals, costals), also on the lateral borders of vertebrals; areolae or areolar areas slightly and irregularly flecked with black, on costals 1-3 and on vertebrals 1-3. Dark patches wider on the plastron, issued from the areolae, roughly extending along the rear third of each scute (from pectorals to anals), restricted to a narrow band on the humerals; limits of the patches are inconspicuous, with a gradual shading, delimiting few lighter or darker radiating lines. Soft parts mostly yellowish, in places with a brownish tinge, with well contrasting blackish flecks on the horny beak (upper and lower, forming a 'moustache'), on prefrontal, on the large triangular scutes of the fore-arms, and on the heels; all nails are also heavily pigmented, from dark brown to black.

Additional morphometric data derived from the neotype are presented in the following (all measurements in mm): maximum plastron length (PL) = 122.7, midline plastron length (PL-m) = 111.8, maximum mid-body width (MI) = 100.2, maximum width of shell at posterior marginals (MA) = 104.4, maximum gular scute length (GU-l) = 15.3, maximum gular scute width (GU-w) = 27.3, gular scute height (GU-h) = 13.2, maximum shell height (HE) = 70.0, maximum width of anterior shell opening (ASO-w) = 69.9, maximum height of anterior shell opening (ASO-h) = 21.9, left minimum bridge length (BR) = 59.9, maximum humeral scute width (HUM-w) = 63.7, maximum pectoral scute width (PEC-w) = 86.6, maximum abdominal scute width (ABD-w) = 89.9, maximum femoral scute width (FEM-w) = 64.1, maximum anal scute width (AN-w) = 51.9, maximum nuchal scute length (NU-l) = 11.4, maximum nuchal scute width (NU-w) = 10.0, intergular length (GU-m) = 13.4, interhumeral length (HUM-m) = 22.8, interpectoral length (PEC-m) = 7.7, interabdominal length (ABD-m) = 42.1, interfemoral length (FEM-m) = 10.8, interanal length (AN-m) = 18.7, maximum width of first vertebral scute (V1-w) = 35.2, maximum width of second vertebral scute (V2-w) = 36.4, maximum width of third vertebral scute (V3-w) = 41.0, maximum width of fourth vertebral scute (V4-w) = 33.8, maximum width of fifth vertebral scute (V5-w) = 41.3, maximum length of first vertebral scute (V1-l) = 26.9,

maximum length of second vertebral scute (V2-l) = 28.0, maximum length of third vertebral scute (V3-l) = 25.6, maximum length of fourth vertebral scute (V4-l) = 23.3, maximum length of fifth vertebral scute (V5-l) = 31.8, first costal length (C1) = 43.0, second costal length (C2) = 28.7, third costal length (C3) = 28.1, fourth costal length (C4) = 22.9, maximum dorsal width of supracaudal (SUP-d) = 23.4, maximum ventral width of supracaudal (SUP-v) = 40.4, maximum median length of supracaudal (SUP-l) = 21.7, maximum head width (HEAD) = 21.6, minimum distance between right eye and tympanum (EYE-TY) = 6.9, minimum distance between right eye and nostril (EYE-NO) = 6.5.

Figure 2 (lower right) depicts a living female (topotype) *Testudo terrestris* Forsskål from the type locality, Aleppo, Syria.

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An *Ocadia sinensis* x *Cyclemys shanensis* hybrid (Testudines: Geoemydidae)

MAIK SCHILDE[1], DANA BARTH[2] AND UWE FRITZ[3]

[1]*Opalstr. 31, D-04319 Leipzig, Germany; E-mail: maik.schilde@ufz.de*

[2]*University of Leipzig, Institute of Zoology, Molecular Evolution & Animal Systematics, Talstr. 33, D-04103 Leipzig, Germany; E-mail: dbarth@rz.uni-leipzig.de*

[3]*Zoological Museum (Museum für Tierkunde), Natural History State Collections Dresden, A. B. Meyer Building, Königsbrücker Landstr. 159, D-01109 Dresden, Germany; E-mail: uwe.fritz@snsd.smwk.sachsen.de*

Abstract. - A captive bred *Ocadia sinensis* x *Cyclemys shanensis* hybrid is described. Its hybrid status was confirmed by a comparison of a 1036 bp fragment of the mitochondrial cytochrome b gene with the putative mother (*C. shanensis*) and genomic ISSR fingerprinting. This is the first report of an intergeneric hybrid between very distantly related geoemydid turtles. All previous geoemydid intergeneric hybrids have been crossings within or between two sister clades containing the currently accepted genera (*Chinemys*, *Mauremys*, *Ocadia*) and (*Cuora*, *Pyxidea*).

Key words. - *Cyclemys*, *Ocadia*, testudines, intergeneric hybrid.

Introduction

Recently several new cases of intergeneric chelonian hybrids became known to science (reviewed in Galgon and Fritz, 2002). Most of them belong to the Southeast Asian family Geoemydidae, long known under its junior synonym Bataguridae. However, current research on the molecular phylogeny of geoemydids has shown that some species traditionally attributed to different genera are more closely related than previously thought (Wu et al., 1999; McCord et al., 2000; Honda et al., 2002a, b; Barth et al., in press; Stuart and Parham, in press), suggesting that they should be better lumped in the same genus. Thus, some of the hybrids may be in fact not intergeneric. In this paper we report a captive bred hybrid between two distantly related Southeast Asian geoemydids, representing an undoubtedly intergeneric cross.

According to the cited studies, there are several major clades among geoemydids. One clade contains the currently recognized genera *Chinemys*, *Mauremys*, *Ocadia*, *Cuora*, and *Pyxidea* (McCord et al., 2000; Honda et al., 2002a, b; Barth et al., in press), and another one, being the sister clade, *Cyclemys*, *Sacalia*, *Heosemys*, *Hieremys*, *Notochelys*, and *Leucocephalon* (McCord et al., 2000; Honda et al., 2002b).

The turtle described herein is the result of a hybridization of an *Ocadia sinensis* male and a *Cyclemys shanensis* female, representatives of two of the major clades of the Geoemydidae. This hybrid demonstrates that very distantly related geoemydids are capable of hybridizing successfully. It underlines the possibility that some recently described Southeast Asian chelonians (*Ocadia glyphistoma*, *O. philippeni*), which are only known from few pet trade specimens, might also be hybrids.

The specimen. - The turtle described below hatched in the live collection of M. Schilde from an egg of a *Cyclemys shanensis*, laid August 13, 2002. The second egg of the same clutch did not develop. The mother was a long term captive, and kept with a *Cyclemys shanensis* male and two *Ocadia sinensis* males. The elongated eggs measured 56.5 x 20.0 mm. One quickly developed a white band as typical for fertile eggs. It was incubated constantly at 28°C on Vermiculite. On October 26, 2002 a healthy turtle with a straight line shell length of 33 mm hatched (Figs. 1-4). Its color pattern resembled *Ocadia sinensis* but the general form was more similar to *Cyclemys* (roofed, distinctly tricarinate shell, serrated posterior marginal scutes), suggesting that it might be a hybrid. We decided to use two molecular methods to test this hypothesis.

Materials and Methods

We sequenced a 1036 bp portion of the mitochondrial cytochrome b gene (cyt b) of the captive bred turtle for comparison with the putative mother. Because mitochondrial DNA is inherited in the maternal line, the sequence of the putative hybrid should be identical with the mother (*Cyclemys shanensis*). Species identification of the *Cyclemys* was done by morphological means and comparison with the mitochondrial cyt b sequences of Guicking et al. (2002); the *Ocadia sinensis* males were determined morphologically.

Blood samples were obtained by coccygeal vein puncture. Samples were stored as described in Haskell

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Figure 1.

Figure 2.

Figure 3.

Figure 4.

Fig. 1-4. The captive bred *Ocadia sinensis* x *Cyclemys shanensis* hybrid, September 2003 (11 months old). The roofed, distinctly tricarinate shell and the serrated posterior marginals resemble *Cyclemys* spp. The neck and facial stripes as well as the plastral pattern are similar to *O. sinensis*. The plastral pattern was more contrasting as a hatchling and has faded during growth. Photos: F. Höhler.

and Pokras (1994) and Arctander (1988). Additional blood samples and photographs (dorsal and ventral aspects) of the captive bred turtle (MTD T1262), the *Cyclemys shanensis* female (MTD T816), and the two *Ocadia sinensis* males (MTD T817-818) are in the tissue collection of the Zoological Museum Dresden. DNA extraction was carried out using the QIAamp Blood Mini Kit (Qiagen). Primers mt-A (Lenk and Wink, 1997) and H15909 (Lenk et al., 1999) were used to amplify a DNA fragment containing 1036 bp of cyt b. PCR and sequencing conditions were as described in Barth et al. (in press). Sequencing reactions were performed on an ABI 3100 Genetic Analyzer. Alignment was carried out with CLUSTAL X, v. 1.8 (Thompson et al., 1997) with default parameters. To demonstrate the considerable genetic difference between *Cyclemys* and *Ocadia* compared to other hybridizing geoemydids, Mega 2.1 (Kumar et al., 2001) was used for estimation of genetic distances. Cyt b sequence data for calculating genetic distances are from Barth et al. (in press) and Guicking et al. (2002).

To exclude the possibility of a gynogenetic or parthenogenetic origin of the specimen and to identify the putative father, we conducted genomic fingerprinting with Inter Simple Sequence Repeats (ISSR) for the captive bred specimen, the *Cyclemys* female and both *Ocadia* males. ISSR PCR produces species-specific genomic fingerprints (Gupta et al., 1994; Zietkiewics et al., 1994; Wink et al., 1998, 2001; Nagy et al., 2003) useful in detecting turtle hybrids (Wink et al., 2001). Hybrid specimens share about 50% of their ISSR PCR products with the respective paternal and maternal species (Wolfe et al., 1998; Wink et al., 2001; Storch et al., 2001). ISSR PCR is a simple and cheap method, and the results are easily reproducible (Bornet and Branchard, 2001). Gynogenesis or pseudogamy, the development of unfertilized eggs by activation through sperm of another species, as well as parthenogenesis is not known in turtles. However, if the captive bred specimen should be of such origin, the ISSR profiles should be identical with its biological mother.

The primer 5´-GACAGACAGACAGACA-3` was used to generate ISSR fingerprints for the captive bred specimen, the putative mother (*Cyclemys shanensis*), and both *Ocadia sinensis* males. Each reaction mix contained 100 ng of genomic DNA, 20 pmol primer, 1 U

Table 1. ISSR fingerprints of the *Ocadia sinensis* x *Cyclemys shanensis* hybrid and parental species (biological mother and father plus the second *O. sinensis* male kept with the mother). Only polymorphic and diagnostic PCR products shown.
MTD T = Museum für Tierkunde Dresden Tissue Collection; + = PCR product present, - = PCR product lacking.

Fragment Length	*Cyclemys shanensis* MTD T816	Hybrid MTD T1262	*Ocadia sinensis* MTD T817	*Ocadia sinensis* MTD T818
100 bp	+	+	-	-
480 bp	-	+	+	+
590 bp	-	+	+	+
810 bp	+	+	-	-
940 bp	+	+	-	-
1100 bp	-	+	+	-
1450 bp	-	+	+	+
1500 bp	+	+	-	-
1550 bp	-	+	+	-
1700 bp	+	+	-	-
2400 bp	-	+	+	+
2700 bp	-	+	+	+
2900 bp	+	+	-	-

Taq-polymerase (SIGMA), 2.5 µl 10x PCR buffer (SIGMA) and 2.5 µl of 200 µM dNTPs in a total volume of 25 µl. Amplification conditions were 4 min initial denaturation (94°C), followed by 31 cycles of 1 min at 94°C, 1 min at 54°C, and 2 min at 72°C, final extension of 7 min (72°C). PCR reactions were performed on an Eppendorf thermocycler.

15 µl of each PCR reaction was separated on 2% agarose gels (25 cm), stained in ethidium bromide solution (0.5 µg/ml) and visualized under UV light. The 100 bp DNA ladder Plus (MBI Fermentas) was used as a size standard. PCR was repeated under identical conditions to test reproducibility of results. DNA fragments were scored manually. Band sharing coefficients were calculated according to Storch et al. (2001).

Results and Discussion

As expected, the cyt b sequence of the captive bred turtle and the putative mother (*Cyclemys shanensis*; EMBL acc. no. AJ604513) proved to be identical. ISSR fingerprinting produced highly variable profiles which were species-specific and permitted individual identification of both *Ocadia sinensis* males (Table 1). The captive bred turtle shared 6 of its 13 bands with the mother (band sharing coefficient 0.5) and 7 bands with one of the *O. sinensis* males (band sharing coefficient 0.52). Because the captive bred turtle and this *O. sinensis* male exclusively share some fragments, we identified this turtle as the biological father. Thus, both methods confirmed the hybrid origin of the captive bred turtle.

Except for an unconfirmed, anecdotal newspaper record of natural hybrids between *Cuora flavomargina-ta* and *Geoemyda japonica* in Japan (Anonymous, 1995), all previous geoemydid intergeneric hybrids have been crossings within or between two sister clades containing the currently accepted genera (*Chinemys*, *Mauremys*, *Ocadia*) and (*Cuora*, *Pyxidea*): *Chinemys reevesii* x *Cuora amboinensis kamaroma* (Galgon and Fritz, 2002), *Chinemys reevesii* x *Mauremys japonica* (Yasukawa et al., 1992), *Chinemys reevesii* x *Mauremys mutica* (= "*Mauremys pritchardi*", Wink et al., 2001), *Cuora amboinensis kamaroma* x *Mauremys annamensis* (Fritz and Mendau, 2002), *Cuora bourreti* x *Pyxidea mouhotii* (= "*Cuora serrata*", Parham et al., 2001; Stuart and Parham, in press), *Cuora galbinifrons* x *Pyxidea mouhotii* (= "*Cuora serrata*", Parham et al., 2001; Stuart and Parham, in press), and *Cuora trifasciata* x *Mauremys mutica* (= "*Mauremys iversoni*", Parham et al., 2001; Wink et al., 2001). *Cyclemys* belongs to another major clade, comprising the genera *Cyclemys*, *Sacalia*, *Heosemys*, *Hieremys*, *Notochelys*, and *Leucocephalon* (McCord et al., 2000). *Cyclemys* is separated by a considerable genetic distance from *Ocadia* (Table 2), surpassing the genetic distances of the other hybridizing geoemydids.

Superficially our hybrid *Ocadia sinensis* x *Cyclemys shanensis* resembles *O. sinensis* due to its striped head and neck and the spotted plastral pattern. This leads to the speculation that the morphologically similar *Ocadia philippeni* McCord and Iverson, 1992 and *O. glyphistoma* McCord and Iverson, 1994 might be also intergeneric hybrids, as earlier suggested by van Dijk (2000), Lau and Shi (2000), Parham and Shi (2001), and Galgon and Fritz (2002). Both species were described on the basis of only a few pet trade turtles (McCord and Iverson, 1992, 1994), and until now no

Table 2. Pairwise genetic distances (cyt b) between hybridizing geoemydid species.

Geomydid species	Cyt b pairwise distances
Chinemys reevesii - Cuora amboinensis	0.104
Chinemys reevesii - Mauremys japonica	0.050
Chinemys reevesii - Mauremys mutica	0.070
Cuora amboinensis - Mauremys annamensis	0.098
Cuora galbinifrons - Pyxidea mouhotii	0.059
Cuora trifasciata - Mauremys mutica	0.104
Ocadia sinensis - Cyclemys shanensis	0.118

additional specimens became known to science. For some individuals of three other pet trade taxa a hybrid status has been unambiguously demonstrated: Two turtles identified as *Mauremys pritchardi* McCord, 1997 proved to be hybrids of *Chinemys reevesii* and *Mauremys mutica* (Wink et al., 2001). Three *Mauremys iversoni* Pritchard and McCord, 1991 originated from crossing *Cuora trifasciata* and *Mauremys mutica* (Parham et al., 2001; Wink et al., 2001), and several *Cuora serrata* Iverson and McCord, 1992, have been demonstrated to be hybrids between *Cuora galbinifrons* and *Pyxidea mouhotii* and of *Cuora bourreti* and *Pyxidea mouhotii* (Parham et al., 2001; Stuart and Parham, in press).

Until now it is unknown whether all specimens of these taxa are of hybrid origin, and if so, whether the crosses occurred in the wild, in captivity, or whether one or the other form might represent a natural, stable hybrid taxon (Parham et al., 2001; Wink et al., 2001). Many Southeast Asian chelonians are facing extinction due to overexploitation (van Dijk et al., 2000). Therefore, many conservation efforts are established around the globe, including CITES listing and captive breeding programs for several species. A correct taxonomy is the prerequisite for any conservation measure. Hence, it is crucial to determine whether the mentioned taxa represent real evolutionary entities and deserve high priority in conservation, this includes also natural hybrid taxa (Allendorf et al., 2001), or whether they are only incidentally occurring hybrids, without any conservation relevance.

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New Data on the Trade and Captive Breeding of Turtles in Guangxi Province, South China

HAITAO SHI[1], ZHIYONG FAN[2], FENG YIN[3], AND ZHIGANG YUAN[4]

[1]*Department of Biology, Hainan Normal University, Haikou , 571158, Hainan Province, P. R. China.*
E-mail:haitao-shi@263.net; Fax: 0898-65890520; Tel: 0898-66752479; 65883521.

[2]*Fauna Division, The Endangered Species Import and Export Management Office of China (CNMA) #18 Hepingli Dongjie, Beijing 100714, P. R. China.*

[3]*Department of Science and Education, China Wildlife Conservation Association, #18 Hepingli Dongjie, Beijing 100714, P. R. China.*

[4]*Department of Biology, Guangxi Medicine University, 530021, Nanning, P.R.China.*

Abstract. - New data on the captive breeding and trade of turtles in Guangxi Province, China, are presented. These data are from four turtle farms and three markets surveyed in May 2002. The scale of captive breeding in Guangxi is larger than previously known. At the same time, the number of wild turtles in the markets may be decreasing. Issues concerning the licensing of turtle farms and the effectiveness of enforcement are discussed.

Key words. - China, Guangxi, turtles, trade, farming.

Introduction

The People's Republic of China is Asia's most significant importer of tortoises and freshwater turtles and more comprehensive studies on its wildlife trade are urgently needed (Li and Li, 1997; van Dijk, et al., 2000). There is a long history of wildlife consumption in Guangxi, and traditional Chinese medicine is as popular as in neighboring Guangdong Province. Li and Li(1997) reported that there are at least 91 species of animals involved in the wildlife trade in Guangxi, mostly turtles and snakes. The sheer volume of the wildlife trade on the border between China and Vietnam is astonishing, and may be unprecedented in the history of international wildlife trade. Guangxi is one of the main corridor for the import and export of wildlife from land and sea into mainland China. Although China has recently increased its level of protection for imported and exported turtles (Meng et al., 2002), the effectiveness of these new measures is not well demonstrated. We report data on four turtle farms and three markets surveyed in late May 2002.

Turtle farms

Shifu turtle farm (Shifu Town, Nanping City). - The turtle farm was founded in 1996, its area is 65 ha. At it's height it included ~70,000 turtles: ~60,000 *Trachemys sripta elegans*, ~7,000 *Pelodiscus sinensis*, and ~600 *Ocadia sinensis*. However during a very heavy flood on July 5, 2001 in the area, almost all the turtles escaped or drowned. The farm is rebuilding, but now includes only ~700 *Mauremys mutica*, ~200 *Palea steindachneri* and ~50 *Cuora trifaciata*.

Quanming wildlife farm (Located at Quanming Town, Daxin County). - The farm began to raise turtles in 1996. It has ~80 *Mauremys mutica* and 47 *Chelydra serpentina*. Their 36 female *Chelydra* lay 30-35 eggs three times every year. So they get more than 3000 eggs every year. They are expanding to include *Macroclemys temminckii*. Besides turtles, the wildlife farm also breed successfully 1800 Tokay Geckos (*Gekko gecko*) and for several decades has also bred the Masked Palm Civet (*Paguma larvata*).

Qingzhou turtle farm 1 (Qingzhou City). - This farm has been raising turtles since 1981, but was not very successful until 1997. In 2001, the farm had ~1000 *Mauremys mutica* and ~300 *Cuora trifaciata*. In the past they also bred *Trachemys scripta elegans*, but switched to *Cuora trifaciata* and *Mauremys mutica* due to the higher price for the two species. The owner of this farm claims that there are dozens more farms in Qingzhou that were founded based stock from his farm. The phenomena of *Mauremys mutica* mixed with *Cuora trifaciata* was found here, mirroring the conditions of a farm in Tunchang, Hainan Province (Shi & Parham, 2001). It was impossible for us to visit the farm without the local officials of Forestry Department forcing the farmer to accept us. The owner prefers to remain secret in order to avoid theft, taxes, and people wanting to borrow money.

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Qingzhou turtle farm 2 (Qingzhou city). - This farm was founded in 1986. It encompasses 4 hectares, and includes ~7,000 *Mauremys mutica*, ~6,000 *Trachemys scripte elegans*, ~2700 *Pelodicus sinensis*, ~800 *Cuora trifaciata*, 200 *Cuora flavomarginata* and 3 *Pelochelys bibroni*. Approximately, 30,000 hatchlings are bred every year. Unlike the owner of the previously reported farm, the owner of this farm, Wusong Ma, is friendly, generous, and open to visitors. Many famous people have visited his turtle farm, including a former Chinese national vice-premier, the Governor of Guangxi, and the Minister of Agriculture Department. Unfortunately, all this attention may have led to a large theft of *Mauremys mutica* in April of 2001. According to the owner of the farm, the value of these turtles was 50,000 USD. Despite this, Mr. Ma remains non-secretive and has even set up at least 20 additional farms.

Remarks on turtle farms. - The senior author (HS) looked over the licenses for captive breeding of turtles at the Forestry Department of Guangxi Province. More than 600 farms (of various sizes, including small breeding operations) were licensed in Guangxi Province. Zou Yi, an official in the Guangxi Forestry Despartment, informed us that another governmental department (Agriculture Department) issues even more licenses for turtle farming, but we do not have these numbers. Moreover, most breeding operations are illegal and not licensed. Consequently, determining the actual number of commercial, often secretive, turtle breeders will require intensive survey and investigation.

Turtle Markets

Nanning Road Trade Market in Nanning City. - Five stalls with 14 species and 194 turtles were found in this market. The species included 58 *Pelodiscus sinensis*, 24 *Pyxidea mouhotii*, 21 *Platysternon megacephalum*, 17 *Mauremys mutica*, 15 *Trachmys scripta elegans*,13 *Cyclemys dentata*, 13 *Palea steindachneri*, 12 *Sacalia quadriocellata*, 8 *Indotestudo elongata*, 4 *Cuora amboinensis*, 4 *Ocadia sinensis*, 2 *Heosemys grandis*, 1 *Hieremys annandalei*, and1 *Orlitia borneensis*.

Dongfeng Market in Qingzhou City. - Three stalls with 9 species and 64 were found in Dongfeng Market in Qingzhou. The species included 19 *Trachmys scripta elegans*, 18 *Indotestudo elongata*, 9 *Manouria impressa*, 5 *Malayemys subtrijuga*, 4 *Cuora amboinensis*, 4 *Pyxidea mouhotii*, 2 *Geoemyda spengleri*, 2 *Heosemys grandis*, and 1 *Cuora galbinifrons*.

Danqing Wholesale Market in Nanning City. - 5 stalls with 4 species and 42 turtles were found in this market. Sixty (71%) of the turtles were *Platysternon megacephalum*. *Platysternon* was sold at every stall. I was told that they came from turtle farms, but they refused to tell where these turtle farms were.

Remarks on turtles. - According to Lu Qi, the vice director of the Wildlife Management Section of the Guangxi Forestry Department, the past three years have seen a sharp decrease in the numbers of turtles in the markets and he attributes this to increased enforcement. This increased enforcement coincides with an ever-growing commercial effort to breed these turtles. For example, Manying Huang (professor of biology at Guangxi Medicine University) states that there are over 3000 families that raise *Cuora trifasciata* in Nanning City. However, the increased level of enforcement has led to many captive-bred turtles also being confiscated. If indiscriminant confiscations continue it could depress the development of captive breeding of turtles in China.

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Recent Records of Turtles and Tortoises from Laos, Cambodia, and Vietnam

BRYAN L. STUART[1,2,3,4,*] AND STEVEN G. PLATT[4,5]

[1]*Field Museum of Natural History, Department of Zoology, Division of Amphibians & Reptiles, 1400 S. Lake Shore Drive, Chicago, Illinois 60605 USA. E-mail: bstuart@fieldmuseum.org*
**Corresponding author and address*

[2]*University of Illinois at Chicago, Department of Biological Sciences (M/C 066), 845 W. Taylor, Chicago, Illinois 60607 USA*

[3]*Wildlife Conservation Society, P.O Box 6712, Vientiane, Lao PDR*

[4]*Wildlife Conservation Society, P.O. Box 1620, Phnom Penh, Cambodia*

[5]*Present address: Department of Math and Science, Oglala Lakota College, P.O. Box 490, Kyle, South Dakota 57752-0490 USA*

Abstract. - The chelonian fauna of Laos, Cambodia, and Vietnam remains poorly known and is currently threatened by widespread and intensive exploitation for food and traditional Chinese medicine. The distributions of many species are uncertain owing to a paucity of records. Because turtles are so extensively traded in the region, most records now come from animals in trade. We emphasize that authors must be explicit about how their records were obtained to allow other workers the ability to critically evaluate the accuracy of the distribution record. We here present detailed information on recent (1993-2002), vouchered records of 19 species of freshwater turtles, tortoises, and marine turtles collected in the field or obtained from hunters, abandoned hunting camps. villages, or markets in Laos, Cambodia, and Vietnam.

Key words. - Testudines, turtles, tortoises, Laos, Cambodia, Vietnam, distribution.

Introduction

Although mainland Southeast Asia has long been regarded as a hotspot of chelonian diversity (van Dijk et al., 2000), the turtle and tortoise fauna of Laos, Cambodia, and Vietnam (formerly known as French Indochina) remains poorly known. Biological investigation was limited prior to World War II, and since then decades of civil unrest, political instability, and military conflict have largely prevented fieldwork. Consequently few museum records exist (summarized by Iverson, 1992) and with the exceptions of Smith (1931) and Bourret (1941), little information is available on the occurrence and distribution of chelonians in former French Indochina. A recent photographic identification guide to the region (Stuart et al., 2001) and country reviews of Laos (Stuart and Timmins, 2000), Cambodia (Touch et al., 2000), and Vietnam (Hendrie, 2000) summarized information on chelonian distributions, but provided few details concerning new records on which these accounts are based.

Exploitation of chelonians for food and medicinal markets is widespread in Laos, Cambodia and Vietnam (Jenkins, 1995; Le Dien Duc and Broad, 1995; Lehr, 1997; Timmins and Khounboline, 1999; van Dijk et al., 2000; Ziegler, 2002; Holloway 2003). Hunters in rural villages capture turtles and tortoises for local consumption or to sell to traders who periodically visit villages to purchase wildlife. Although turtles and tortoises are locally consumed and domestically traded in Laos, Cambodia, and Vietnam, most are exported to markets in southern China (Stuart et al., 2000; van Dijk et al., 2000). Chelonians from Laos and Cambodia are usually transported to Vietnam, where they join with Vietnamese turtles on northward routes to China (Stuart et al., 2000). Because Laos and Cambodia are source rather than destination or transfer countries, specimens obtained from markets in Laos or Cambodia usually originated from that country. However, trade specimens in Vietnam may have originated from Vietnam, Laos, Cambodia, or beyond. The volume of this trade is believed to pose a serious threat to the continued viability of wild chelonian populations throughout Southeast Asia (van Dijk et al., 2000).

Because turtles and tortoises are extensively and visibly traded in Southeast Asia, most recent distribution records are based on animals observed in trade rather than collected from the wild. The geographic origin of many trade specimens can be difficult if not impossible to determine, especially those obtained in urban markets. Uncritical acceptance of these records by workers has led to inaccurate characterization of species distributions, with serious biological, conservation, legal, and regulatory implications. Additional confusion has result-

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ed from the realization that some species of Asian turtles described during the last two decades were based on type specimens obtained from Hong Kong animal dealers who provided inaccurate or fabricated locality data, leaving the geographic origin of many in doubt (Dalton, 2003; Parham et al., 2001). Distribution records that explicitly state how the turtles were obtained are therefore clearly important, given the historical paucity of information, uncertainties in recent literature, and the serious conservation threats faced by these taxa.

We here report recent distribution records of chelonians from Laos, Cambodia, and Vietnam that can be verified with voucher specimens or photographs. These records were obtained by (1) us during herpetological surveys conducted from February 1998 through May 2001, (2) other workers in the region between 1993 and June 2002, and provided to us, or (3) other workers who deposited specimens at the Field Museum of Natural History, Chicago, USA since 1993. For each record we note whether the specimen was collected in the field, found in abandoned hunting camps, obtained from hunters or residents in rural villages, or purchased from markets.

It should be emphasized that our collecting activities had little if any detrimental impact on populations of wild chelonians. The number of collected specimens on which we report is insignificant when compared to the millions of chelonians annually consumed by the wildlife markets of southern China (Lau et al., 2000). Furthermore, the majority of specimens we and others collected in the field were shells of animals consumed by rural villagers. Chelonian shells are commonplace and easily obtained in villages; shells are retained by hunters as trophies, sold or kept for medicinal purposes, and used as food containers for domestic animals and rice scoops. Our collecting activities certainly provided no stimulus for the additional harvesting of wild chelonians. Finally, we believe that further scientific collecting is warranted in the region, as most species remain under-represented in museum collections, and taxonomic study can affect conservation priorities (Parham and Shi, 2001; Stuart and Thorbjarnarson, 2003).

Methods and Conventions

Measurements were taken to the nearest 0.1 cm with 80 cm sliding calipers. We use the following abbreviations: CL = maximum straight carapace length, including spines or projections (i.e. not necessarily the mid-line); CW = maximum carapace width, including spines or projections; PL = maximum plastron length, including spines or projections; BD = maximum depth of complete specimen (head and neck extended in trionychid specimens). Measurements were not reported if shell damage precluded accurate measurement.

Records are presented under each species account in the following format where applicable: Field Museum of Natural History (FMNH) or figure number, type of record, measurements (defined above), locality including coordinates if available, approximate elevation and brief habitat description if field-collected, circumstances of origin if not field-collected by collector or photographer, date specimen was collected or photographed, and name of collector or photographer. In the case of records obtained from hunters or villages, the name of collector refers to the person who preserved the specimen or provided the record to us rather than to the name of the person who actually captured it from the wild. In the same cases, the date of collection refers to the date the collector (as previously defined) obtained the specimen or took the photograph rather than to the date it was removed from the wild.

GPS coordinates are presented only if the original collector provided them, and in the same format as originally provided. Coordinates that we generated for the purposes of mapping the records are not presented. Marine turtle records are not mapped.

Species Accounts

Platysternidae

Platysternon megacephalum Gray, 1831
[Map 1]

Laos. - **Fig. 1**, photograph only, Huaphahn Province, Vieng Tong District, Ban Sa Kok Village, 20°11' N 103°12' E, captured by resident of Ban Sa Kok, 29 April 1998, B. L. Stuart. **FMNH 258749**, complete specimen, CL = 9.3, CW = 7.3, PL = 6.9, BD = 2.6, Bolikhamxay Province, Khamkeut District, Nape border area, stream in wet evergreen forest, 19 March 1997, D. Davenport. **Fig. 2** (and Fig. 4 in Stuart and Timmins, 2000), photograph only, Khammouan Province, Nakai District, Nakai-Nam Theun National Biodiversity Conservation Area, Ban Xiangthong Village, 17° 54' 05" N 105° 23' 50" E, one of eleven individuals in the possession of a Vietnamese trader leaving Ban Xiangthong, 17 November 1998, B. L. Stuart. **Fig. 3**, photograph only, Xe Kong Province, Dakchung District, Ban Daklan Village, 15° 21.61' N 107° 01.70' E, captured by residents of Ban Daklan, D. Showler, December 1997. **Vietnam**. - **FMNH 252164**, complete specimen, CL = 15.5, CW = 11.6, PL =12.7, BD = 5.2, Gia-Lai Province, Ankhe District, Buon Loi Village, 20 km northwest of Kannack town, Annamite Mountains, 14° 20' N 108° 36' E, 700-750 m, found in burrow under overhanging stream bank, 31 March 1995, I. Darevsky and N. L. Orlov.

Remarks. - Ziegler (2002) reported the species in local trade in Ha Tinh Province, Vietnam.

Geoemydidae

Batagur baska (Gray, 1831 "1830-35")
[Map 2]

Cambodia. - Platt et al. (2003) reviewed the status of *B. baska* in Cambodia and reported on a breeding population in the Sre Ambel River System of Koh Kong Province.

Cuora amboinensis (Daudin, 1802)
[Map 3]

Cambodia. - **Fig. 4**, photograph only, Battambang Province, Ek Phnom District, Koh Chivang Commune, Prek Toal Village on Tonle Sap Lake, 13°14' 28" N 103° 39' 32" E, captured by residents of Prek Toal, 27 August 1999, B. L. Stuart, J. Smith, and K. Davey. **FMNH 259411**, broken carapace and plastron, Kandal Province, Trayo Village, 11° 19' 02" N 105°09' 47" E, obtained from hunter in Trayo, 05 July 2000, S. G. Platt. **Fig. 5**, photograph only, two living turtles, CL = 19.3 and PL = 17.5, CL = 20.6 and PL = 18.9, Kampong Thom Province, Sary Village, 12° 48.48' N 104° 44.19' E, collected by Sary residents in Tonle Sap, 21 June 2000, S. G. Platt, Heng Sovannara, and Long Kheng. **Fig. 6**, photograph only, CL = 20.4 cm, PL = 18.5, Koh Kong Province, Sre Ambel Town, in house of wildlife trader, 11° 07.30' N; 103° 44.73' E, 27 August 2000, S. G. Platt, B. L. Stuart, and Vuthy Monyrath. **Fig. 7**, photograph only, CL = 11.6, PL = 11.0, Koh Kong Province, Koh Kong Town near municipal airport, 11° 37.11' N; 103° 00.98' E, crossing road in open grassland bordered by *Melaleuca* and *Rhizophora* swamp, 07 February 2001, S. G. Platt, Heng Sovannara, and Long Kheng.
Laos. - **FMNH 255262**, complete specimen, CL = 16.7, CW = 11.7, PL = 15.2, BD = 7.5, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, Ban Khiem Village, 14°14' N 105° 20' E, captured by residents of Ban Khiem for food, 24 July 1998, B. L. Stuart.
Vietnam. - **Fig. 8**, photograph only, Kien Giang Province, An Minh District, photographed in a reptile trade shop, 09° 45' 04" N 104° 59' 35" E, 31 October 2000, B. L. Stuart.

Cuora galbinifrons Bourret, 1939
[Map 4]

Laos. - **FMNH 256544**, complete specimen, CL = 16.6, CW = 12.2, PL = 16.2, BD = 8.0, Khammouan Province, Nakai District, Nakai-Nam Theun National Biodiversity Conservation Area, 17° 50' N 105° 35' E, 900 m, wet evergreen forest, found under brush in leaf litter on hillside 500 m from nearest stream, 13 December 1998, B. L. Stuart. **FMNH 255273**, carapace only, CL = 18.1, CW = 12.9, Khammouan Province, Yommalat District, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban That Mouang Khai Village, 17° 32' N 105° 04' E, consumed by residents of Ban That Mouang Khai, 01 April 1998, B. L. Stuart.
Vietnam. - **FMNH 255694**, complete specimen, CL = 19.2, CW = 13.0, PL = 18.0, BD = 8.5, Nghe An Province, Tuong Duong District, Pu Mat Nature Reserve, 19° 03' N 104° 37' E, 600 m, wet evergreen hill forest, in leaf litter along Khe Mat Stream, 14 September 1998, B. L. Stuart. **FMNH 255695**, complete specimen, repatriated to Vietnam before measurements could be taken, collecting information same as FMNH 255694.

Remarks. - The subspecies *C. galbinifrons galbinifrons* Bourret, 1939 is treated here as a full species following the recommendation of Stuart and Parham (2004). Ziegler (2002) reported the species in local trade in Ha Tinh Province, Vietnam, and Fritz et al. (2002) reported hybrids of *C. galbinifrons* and *C. bourreti* in local trade in Ha Tinh and Quang Binh Provinces, Vietnam.

Cuora mouhotii (Gray, 1862)
[Map 5]

Laos. - **FMNH 258880**, carapace only, CL = 16.1, CW = 11.0, Khammouan Province, Boualapha District, Hin Nam No National Biodiversity Conservation Area, Ban Tasang Village, eaten by residents of Ban Tasang, 30 December 1995, R. J. Timmins. **FMNH 258881**, carapace only, CL = 17.3, CW = 13.0, collecting information same as FMNH 258880. **FMNH 258887**, plastron only, PL = 16.8, Bolikhamxay Province, Nam Kading National Biodiversity Conservation Area, eaten by villagers living in Nam Kading, 01 May 1995, R. J. Timmins.

Remarks. - The species *mouhotii* was previously placed in the monotypic genus *Pyxidea* Gray, 1863, but we allocate it to the genus *Cuora* following Honda et al. (2002) and Stuart and Parham (2004). Ziegler (2002) reported the species in local trade in Ha Tinh Province, Vietnam.

Cyclemys atripons Iverson and McCord, 1997
[Map 6]

Cambodia. - **FMNH 259050**, complete specimen, CL = 21.4, CW = 16.2, PL = 20.7, BD = 8.4, Mondolkiri Province, Pichrada District, Phnom Nam Lyr Wildlife

Sanctuary, near 12° 32' 16" N 107° 32' 00" E, 600-700 m, evergreen gallery forest, found on sand bank at base of large boulder 1.5 m from swift, shallow stream, 21 June 2000, B. L. Stuart. **FMNH 259051**, complete specimen, CL = 22.7, CW = 17.0, PL = 21.2, BD = 8.0, Koh Kong Province, Sre Ambel District, Sre Ambel Town, 11° 07' 20" N 103° 44' 45" E, obtained from turtle trader who reported specimen came from Sophat Village, downstream from Sre Ambel Town, 27 August 2000, B. L. Stuart and S. G. Platt. **FMNH 259052**, complete specimen, CL = 18.0, CW = 15.0, PL =16.7, BD = 6.2, collecting information same as FMNH 259051. **FMNH 259412**, carapace and incomplete plastron, CL = 19.3, CW = 15.2, Koh Kong Province, Sre Ambel District, Boeung Tradok Pong Village, 11° 31' 10" N 103° 46' 55" E, obtained from hunter in Boeung Tradok Pong, 24 August 2000, B. L. Stuart and S. G. Platt. **FMNH 259414**, plastron only, PL = 16.5, collecting information same as FMNH 259412. **FMNH 259415**, plastron only, PL = 16.2, collecting information same as FMNH 259412. **FMNH 259416**, plastron only, PL = 14.9, Koh Kong Province, Sre Ambel District, Chaouethail Plous Village on Sre Ambel River, 11° 18' 03' N, 103° 44' 56"E, obtained from hunter in Chaouethail Plous, 21 August 2000, B. L. Stuart and S. G. Platt. **FMNH 259417**, plastron only, PL = 19.2, collecting information same as FMNH 259416. **FMNH 259422**, plastron only, PL = 20.2, Koh Kong Province, Sre Ambel District, Chay Reap Village, west bank of Sre Ambel River, 11° 29' 10" N 103° 47' 00" E, <10 m, obtained from hunter in Chay Reap, 23 August 2000, B. L. Stuart and S. G. Platt. **Fig. 9**, photograph only, two living animals, CL = 13.7 cm and PL = 13.0 cm, CL = 20.8 cm and PL = 19.6 cm, Koh Kong Province, Kaoh Pao River, 11° 44.46' N; 103° 04.80' E, surrounding hills covered in dense evergreen forest with some mangrove along shoreline, obtained from fishermen, taken in crab traps set in river, 10 May 2001, S. G. Platt, Heng Sovannara, and Long Kheng.

Remarks. - Fritz and Ziegler (1999) reviewed records of *Cyclemys* from the region. Species boundaries within the genus *Cyclemys* remain uncertain (Fritz and Ziegler, 1999; Guicking et al., 2002). The specimens we assigned to *C. atripons* have plastra that are largely yellow with densely pigmented bridges; complete specimens exhibit nearly immaculate chins. These characteristics are typical of both *C. atripons* and *C. pulchristriata* Fritz, Gaulke & Lehr, 1997, two species that were described almost concurrently in 1997. *Cyclemys atripons* and *C. pulchristriata* have been considered the same taxon (Iverson in Guicking et al., 2002). However, Fritz et al. (2001) concluded that *C. atripons* has more ventral neck stripes (7-8 light and 7-9 dark stripes when counted from one mouth corner to the other) than *C. pulchristriata* (5-7 light and 5-7 dark stripes). FMNH 259050 has 8 dark and 7 light ventral neck stripes, FMNH 259051 has 10 dark and 9 light ventral neck stripes, but in FMNH 259052 the ventral side of the neck is nearly immaculate like the chin and completely lacks striping. These few samples demonstrate that ventral neck stripes are more variable than stated by Fritz et al. (2001). In a phylogenetic analysis of a 982 bp fragment of the mitochondrial cytochrome *b* gene, Guicking et al. (2002) recovered two clades in the *atripons-pulchristriata* complex that differed by up to 4.5% sequence divergence. Samples referred to *atripons* and *pulchristriata* appeared in both clades, but the authors assigned these names according to whether the sample originated from Cambodia (*atripons*) or Vietnam (*pulchristriata*), rather than based on their morphology. The findings of Guicking et al. (2002) suggest that more than one species of *Cyclemys* with mostly yellow plastra, densely pigmented bridges, and immaculate chins could exist, but it remains unclear whether the two clades correspond to what have been described as *atripons* and *pulchristriata*. We assign the name *C. atripons* rather than *C. pulchristriata* to our samples because the type locality of *C. atripons* is geographically closer to most of our samples than to that of *C. pulchristriata*. Clearly, further studies into the morphological and genetic variation in *Cyclemys* are warranted, particularly with samples of certain provenance.

Cyclemys tcheponensis (Bourret, 1939)

[Map 7]

Laos. - **Fig. 10** (and Fig. 7d in Stuart et al., 2001), photograph only, Bolikhamxay Province, Thaphabat District, Phou Khao Khouay National Biodiversity Conservation Area, near That Xay Waterfall, 18° 27' N 103° 10' E, 300 m, dry evergreen forest mixed with bamboo, sleeping on bottom of 4 x 4 m pool in forested stream, 26 June 1998, B. L. Stuart. **FMNH 258870**, complete specimen, CL = 9.7, CW = 8.0, PL = 8.7, BD = 3.6, Bolikhamxay Province, Khamkeut District, purchased in Lac Xao Market, 14 December 1996, D. Davenport. **FMNH 258871**, complete specimen, CL = 9.0, CW = 8.1, PL = 8.3, BD = 3.6, collecting information same as FMNH 258870. **FMNH 258875**, complete specimen, CL = 20.6, CW = 15.2, PL = 20.3, BD = 8.5, Khammouan Province, Nakai District, Houay Moey Stream (tributary of Nam Pheo River), Ban Na Meo Village, dry evergreen forest, 07 March 1997, D. Davenport and J. Chamberlain. **FMNH 255263**, complete specimen, CL = 17.1, CW = 13.6, PL = 16.1, BD = 6.5, Khammouan Province, Nakai District, Khammouan Limestone (= Phou Hin Poun) National Biodiversity

Conservation Area, 17° 53' N 104° 52' E, 570 m, dry evergreen forest mixed with deciduous trees and pine, caught on streambank by hunter using dog, 26 March 1998, B. L. Stuart and T. Chan-ard.

Remarks. - Species boundaries within the genus *Cyclemys* remain uncertain (Fritz and Ziegler, 1999; Guicking et al., 2002). The specimens we assigned to *C. tcheponensis* have dark radiating patterns of the plastra, pigmented chins, head and neck stripes, and dorsal spotting on the crown of the head, as illustrated by Fritz and Ziegler (1999) and Fritz et al. (1997). Fritz and Ziegler (1999) reviewed records of *Cyclemys* from the region, and Ziegler (2002) reported the species in local trade in Ha Tinh Province, Vietnam.

Cyclemys sp.
[Map 8]

Cambodia. - **FMNH 259418**, carapace only, CL = 19.5, CW = 14.7, Kampong Speu Province, Koh Kong Samling Logging Concession, 11° 24' 15" N 103° 49' 47" E, 200 m, recovered from hunter's camp, mixed deciduous forest and grassland, 15 February 2000, J. Walston. **FMNH 259419**, carapace only, CL = 22.1, CW = 16.1, collecting information same as FMNH 259418. **FMNH 259420**, carapace only, CL = 19.1, CW = 15.9, collecting information same as FMNH 259418. **FMNH 259421**, plastron only, PL = 21.2, collecting information same as FMNH 259418. **FMNH 259423**, plastron only, PL = 21.0, Koh Kong Province, Sre Ambel District, Chay Reap Village, west bank of Prek Sre Ambel River, 11° 29' 10" N 103° 47' 00" E, <10 m, obtained from hunter in Chay Reap, 23 August 2000, B. L. Stuart and S. G. Platt.
Laos. - **FMNH 258893**, carapace only, CL = 21.8, CW = 16.6, Champasak Province, Pakxong District, Ban Latsasin Village, near Xe Nam Noy River, 800 m, eaten by residents of Ban Latsasin Village, 02 April 1995, T. D. Evans.

Remarks. - The condition of these shell fragments precludes identifying them to species. They are not necessarily a species different from *atripons* or *tcheponensis*.

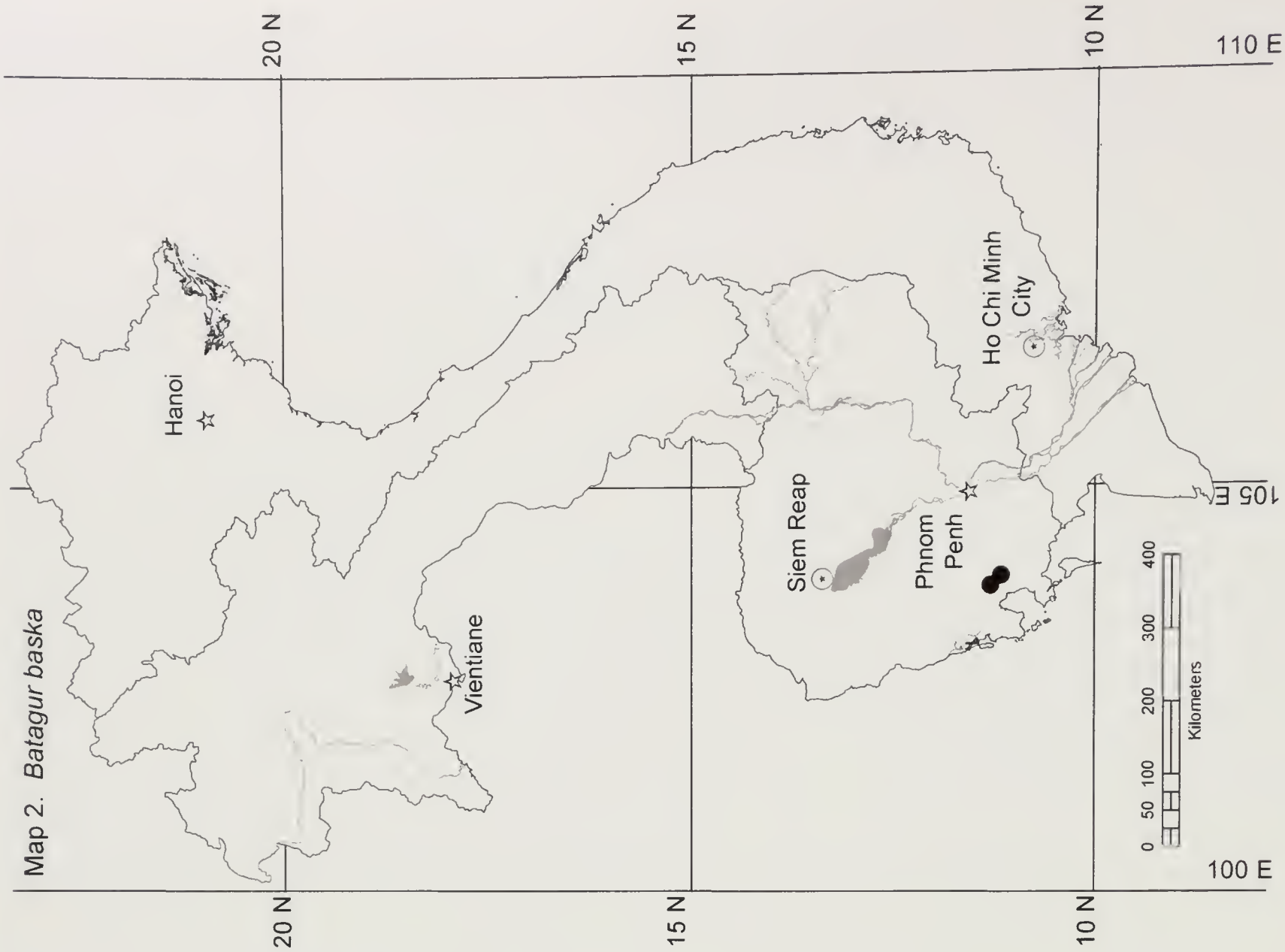
Heosemys grandis (Gray, 1860)
[Map 9]

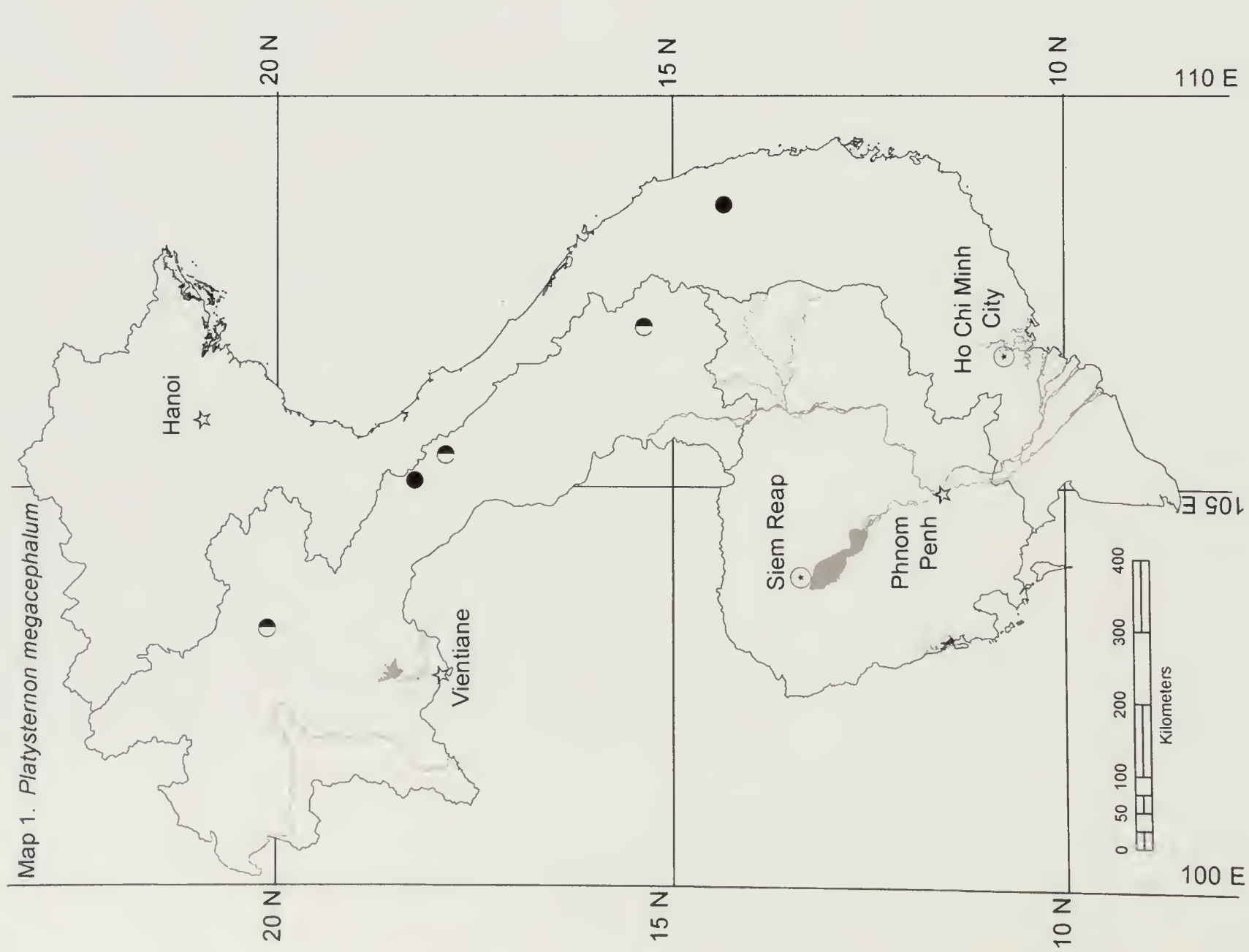
Cambodia. - **FMNH 259409**, carapace only, CL = 30.5, CW = 22.6, Phnom Penh, Oreussay Market, purchased in market, 17 May 1999, S. G. Platt. **FMNH 259405**, plastron only, PL = 26.5, Koh Kong Province, Sre Ambel District, Boeung Tradok Pong Village, 11° 31' 10' N 103° 46' 55" E, obtained from hunter in Boeung Tradok Pong, 24 August 2000, B. L. Stuart and S. G. Platt. **FMNH 259406**, plastron only, PL = 20.8, Koh Kong Province, Sre Ambel District, Chaouethail Plous Village on Sre Ambel River, 11° 18' 03" N 103° 44' 56" E, obtained from hunter in Chaouethail Plous, 21 August 2000, B. L. Stuart and S. G. Platt. **Fig. 11**, photograph only, CL = 31.8, PL = 28.6, Koh Kong Province, Thmor Andart Village along Stoeng Metoek River, 11° 49.23' N, 102° 53.62' E, captured by residents of Thmor Andart, 10 May 2001, S. G. Platt, Heng Sovannara, and Long Kheng. **FMNH 259407**, plastron only, PL = 19.4, collecting information same as FMNH 259406.
Laos. - **FMNH 255271**, carapace only, CL = 23.6, CW = 18.3, Khammouan Province, Thakhek District, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban Na Village, 17° 33' N, 104° 52' E, eaten by residents of Ban Na, 02 April 1998, B. L. Stuart. **FMNH 258885**, plastron only, PL = 27.0, Khammouan Province, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban Namphick Village, eaten by residents of Ban Namphick, 22 May 1994, R. J. Timmins. **FMNH 258894**, carapace only, CL = 36.3, CW = 24.7, collecting information same as FMNH 258885. **FMNH 258889**, plastron only, PL = 13.9, Laos, Khammouan Province, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban Chocksavang Village, eaten by residents of Ban Chocksavang, 22 May 1994, R. J. Timmins. **FMNH 258882**, carapace only, CL = 23.2, CW = 19.1, Savannakhet Province, Thaphangthong District, Xe Bang Nouan National Biodiversity Conservation Area, Ban Houay Meun Village, eaten by residents of Ban Houay, 20 June 1994, R. J. Timmins. **FMNH 258883**, carapace (broken) and plastron only, PL = 36.6, collecting information same as FMNH 258882 except collected 19 June 1994. **FMNH 258877**, carapace only, CL = 34.1, CW = 24.2, Salavan Province, Toumlan District, Xe Bang Nouan National Biodiversity Conservation Area, Ban Nalan Village, eaten by residents of Ban Nalan, 15 June 1994, R. J. Timmins. **FMNH 258878**, intact shell only, CL = 36.8, CW = 25.8, PL = 35.3, BD = 14.7, Salavan Province, Xe Bang Nouan National Biodiversity Conservation Area, Ban Konglur Village, eaten by residents of Ban Konglur, 10 June 1994, R. J. Timmins. **FMNH 258891**, carapace only, CL = 17.3, CW = 15.1, Salavan Province, Xe Bang Nouan National Biodiversity Conservation Area, Ban Nasompeng Village, eaten by residents of Ban Nasompeng, 09 June 1994, R. J. Timmins. **FMNH 258890**, carapace (broken) only, CL = 19.4, Champasak Province, Pathoumphon District, Xe Pian National Biodiversity Conservation Area, Xe Pian River upstream from Ban Phonsaat Village, 100 m, discarded in camp along Xe Pian River

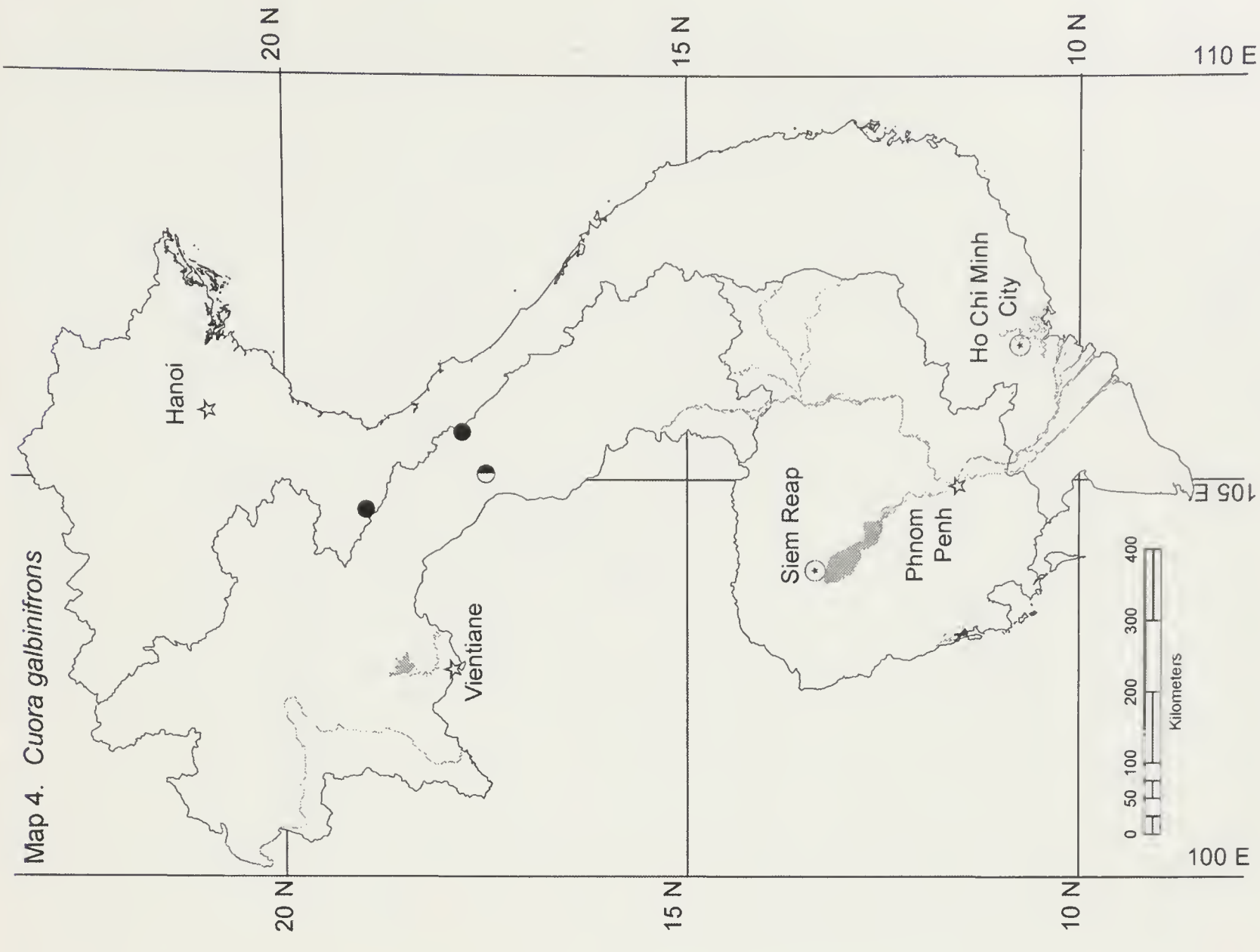
Figures 1-15. See text for locality details and circumstances of the record. 1. *Platysternon megacephalum* Huaphahn Province, Laos (photo B. L. Stuart); 2. *Platysternon megacephalum* Khammouan Province, Laos (photo B. L. Stuart); 3. *Platysternon megacephalum* Xe Kong Province, Laos (photo D. Showler); 4. *Cuora amboinensis* Battambang Province, Cambodia (photo B. L. Stuart); 5. *Cuora amboinensis* Kampong Thom Province, Cambodia (photo S. G. Platt); 6. *Cuora amboinensis* Koh Kong Province, Cambodia (photo S. G. Platt); 7. *Cuora amboinensis* Koh Kong Province, Cambodia (photo S. G. Platt). 8. *Cuora amboinensis* Kien Giang Province, Vietnam (photo B. L. Stuart); 9. *Cyclemys atripons* Koh Kong Province, Cambodia (photo S. G. Platt); 10. *Cyclemys tcheponensis* Bolikhamxay Province, Laos (photo B. L. Stuart); 11. *Heosemys grandis* Koh Kong Province, Cambodia (photo S. G. Platt); 12. *Hieremys annandalii* Battambang Province, Cambodia (photo B. L. Stuart); 13. *Hieremys annandalii* Siem Reap Province, Cambodia (photo S. G. Platt); 14. *Hieremys annandalii* Kampong Thom Province, Cambodia (photo S. G. Platt); 15. *Malayemys subtrijuga* Battambang Province, Cambodia (photo B. L. Stuart).

Figures 16-27. See text for locality details and circumstances of the record. 16. *Malayemys subtrijuga* Kampong Thom Province, Cambodia (photo S. G. Platt); 17. *Malayemys subtrijuga* Kandal Province, Cambodia (photo S. G. Platt); 18. *Malayemys subtrijuga* Vientiane, Laos (photo W. G. Robichaud). 19. *Manouria impressa* Koh Kong Province, Cambodia (photo S. G. Platt). 20. *Manouria impressa* Ratanakiri Province, Cambodia (photo Suon Phalla/TRAFFIC). 21. *Manouria impressa* Xe Kong Province, Laos (photo B. L. Stuart). 22. *Chelonia mydas* Kampong Speu Province, Cambodia (photo B. L. Stuart). 23. *Eretmochelys imbricata* Sihanoukville Province, Cambodia (photo S. G. Platt). 24. *Dermochelys coriacea* Gulf of Thailand, near Sihanoukville, Cambodia (photo Vanna Nhem). 25. *Amyda cartilaginea* Koh Kong Province, Cambodia (photo S. G. Platt). 26. *Amyda cartilaginea* Khammouan Province, Laos (photo B. L. Stuart). 27. *Pelochelys cantorii* Kratie Province, Cambodia (photo D. Gambade).

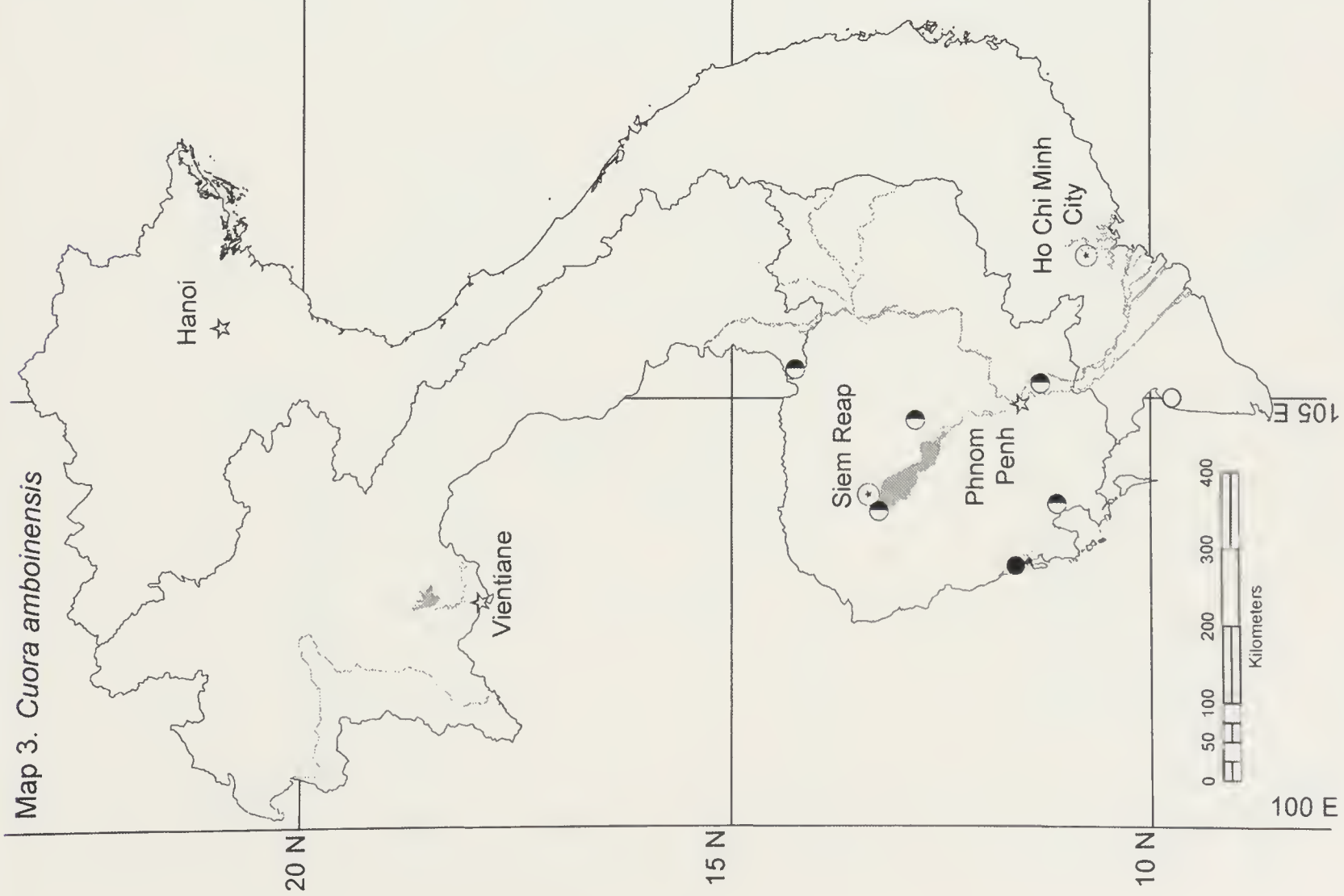
after being eaten by hunters, May 1995, T. D. Evans. **FMNH 255266**, complete specimen, CL = 7.5, CW = 6.4, PL = 6.2, BD = 2.5, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, 14° 07' N 105° 29' E, 60 m, grassland with dry dipterocarp and evergreen forest along Xe Lepou River, found in mud at bottom of flooded marsh, water depth about 15 cm, 11 July 1998, B. L. Stuart. **FMNH 255272**, carapace only, CL = 28.6, CW = 22.2, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, Ban Thahin Village, on Xe Lepou River, 14° 08' N 105° 35' E, 60 m, eaten by residents of Ban Thahin, 17 July 1998, B. L. Stuart.


Map 2. Batagur baska
20 N
15 N
10 N
110 E
105 E
100 E
Hanoi
Vientiane
Siem Reap
Phnom Penh
Ho Chi Minh City
0 50 100 200 300 400
Kilometers


Map 1. Platysternon megacephalum
20 N
15 N
10 N
110 E
105 E
100 E
Hanoi
Vientiane
Siem Reap
Phnom Penh
Ho Chi Minh City
0 50 100 200 300 400
Kilometers



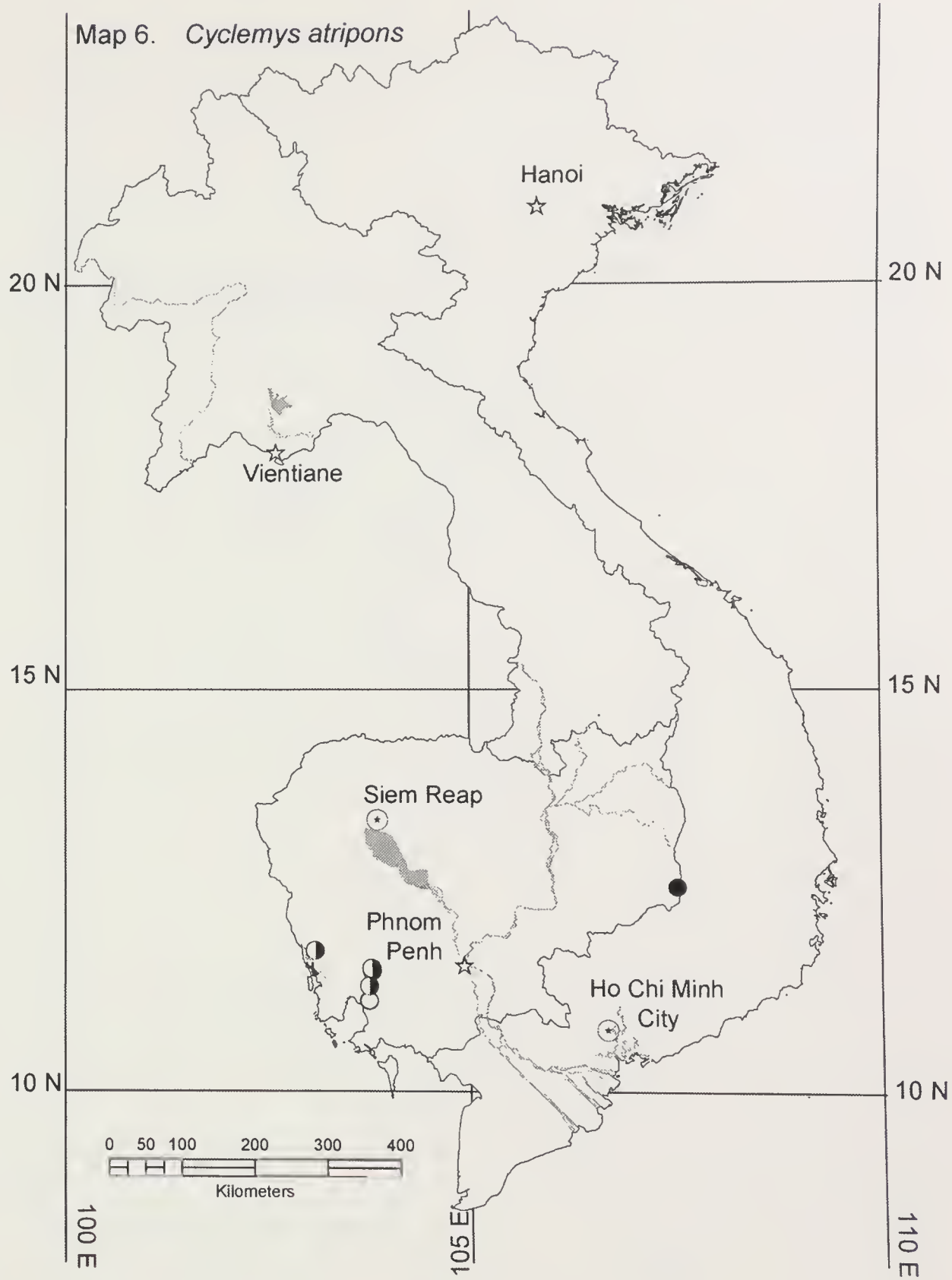
Map 4. *Cuora galbinifrons*



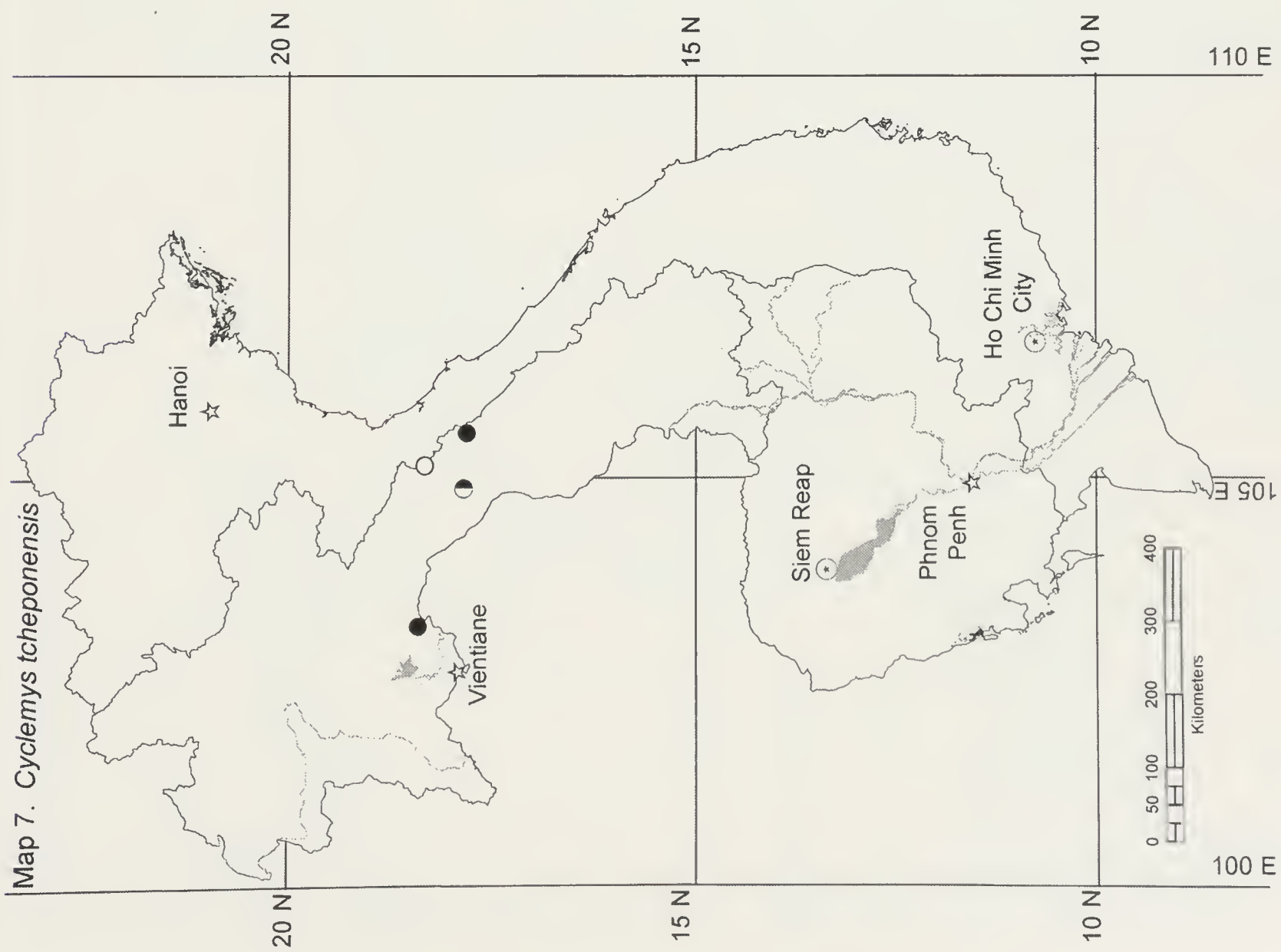
Map 3. *Cuora amboinensis*

Map 5. *Cuora mouhotii*

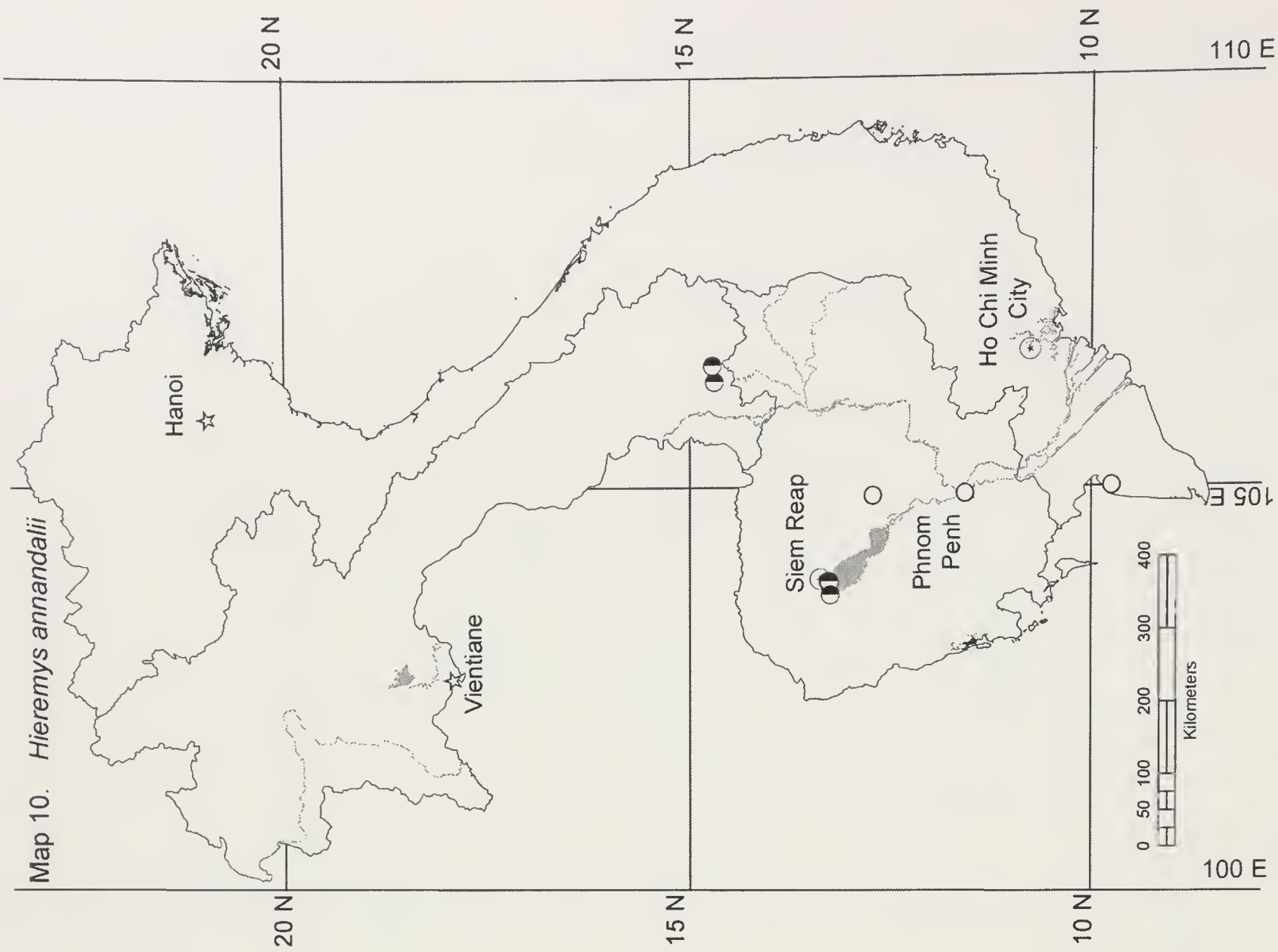
Map 6. *Cyclemys atripons*



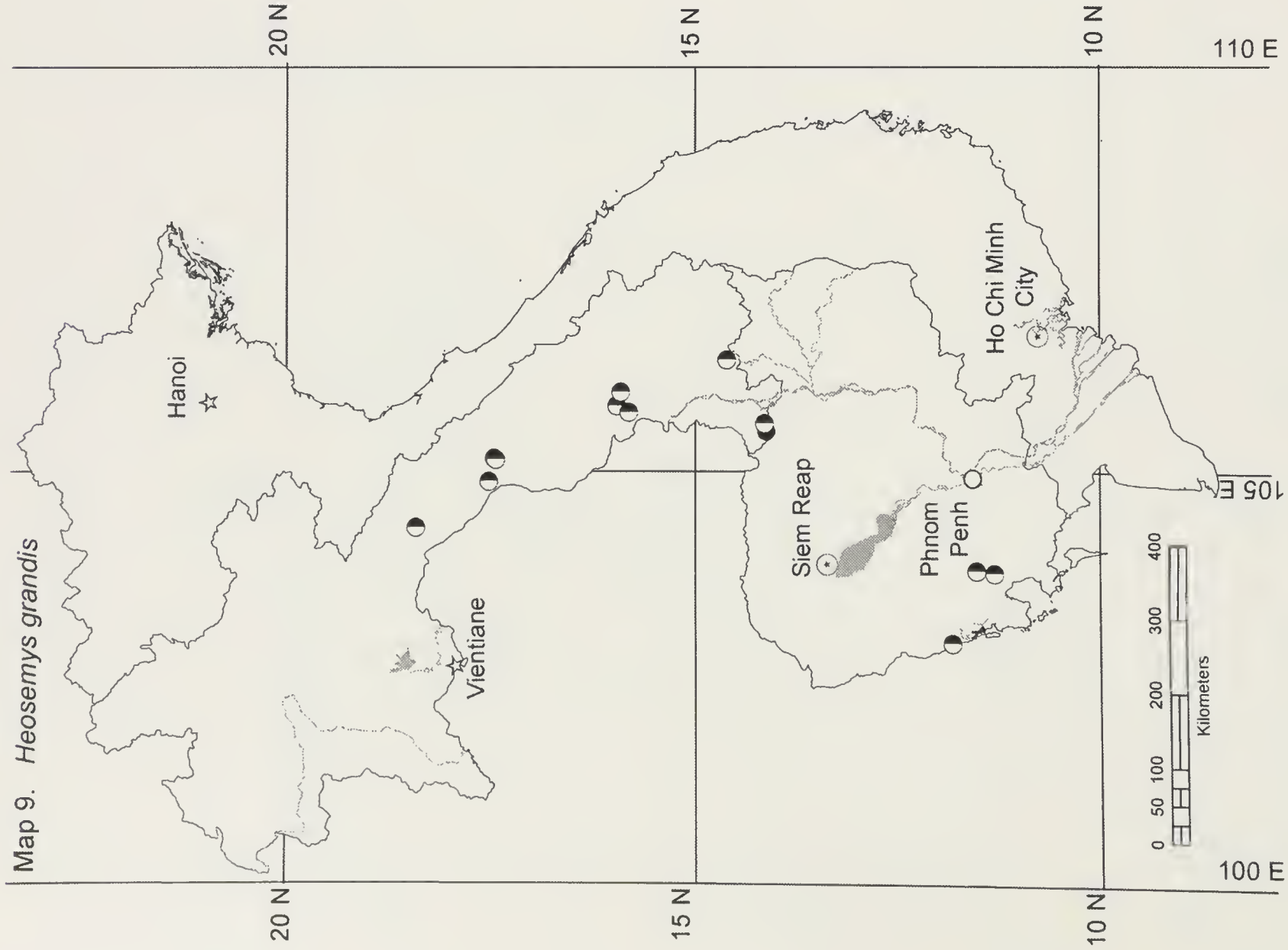
Map 8. *Cyclemys* sp.



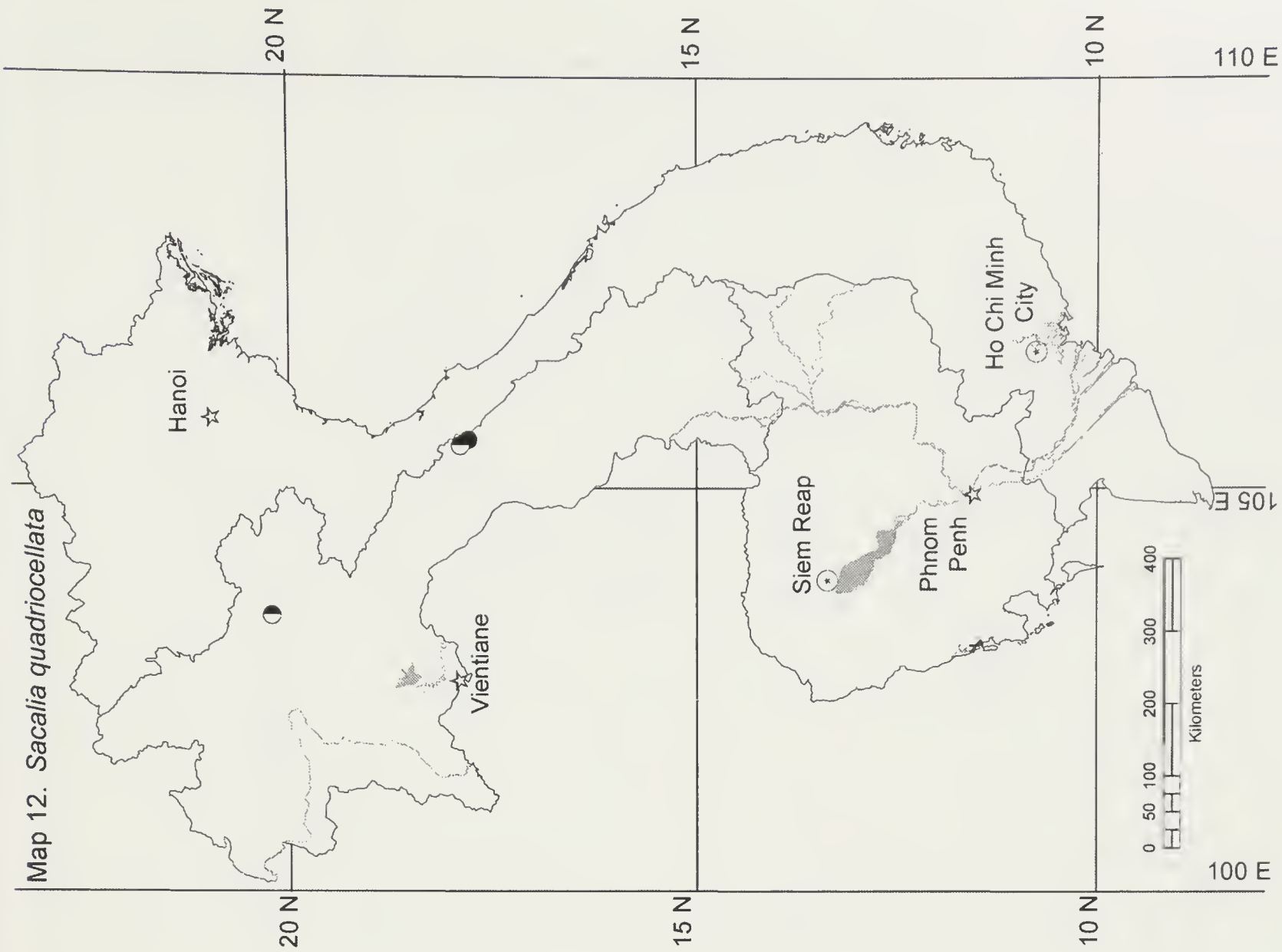
Map 7. *Cyclemys tcheponensis*



Map 10. *Hieremys annandalii*

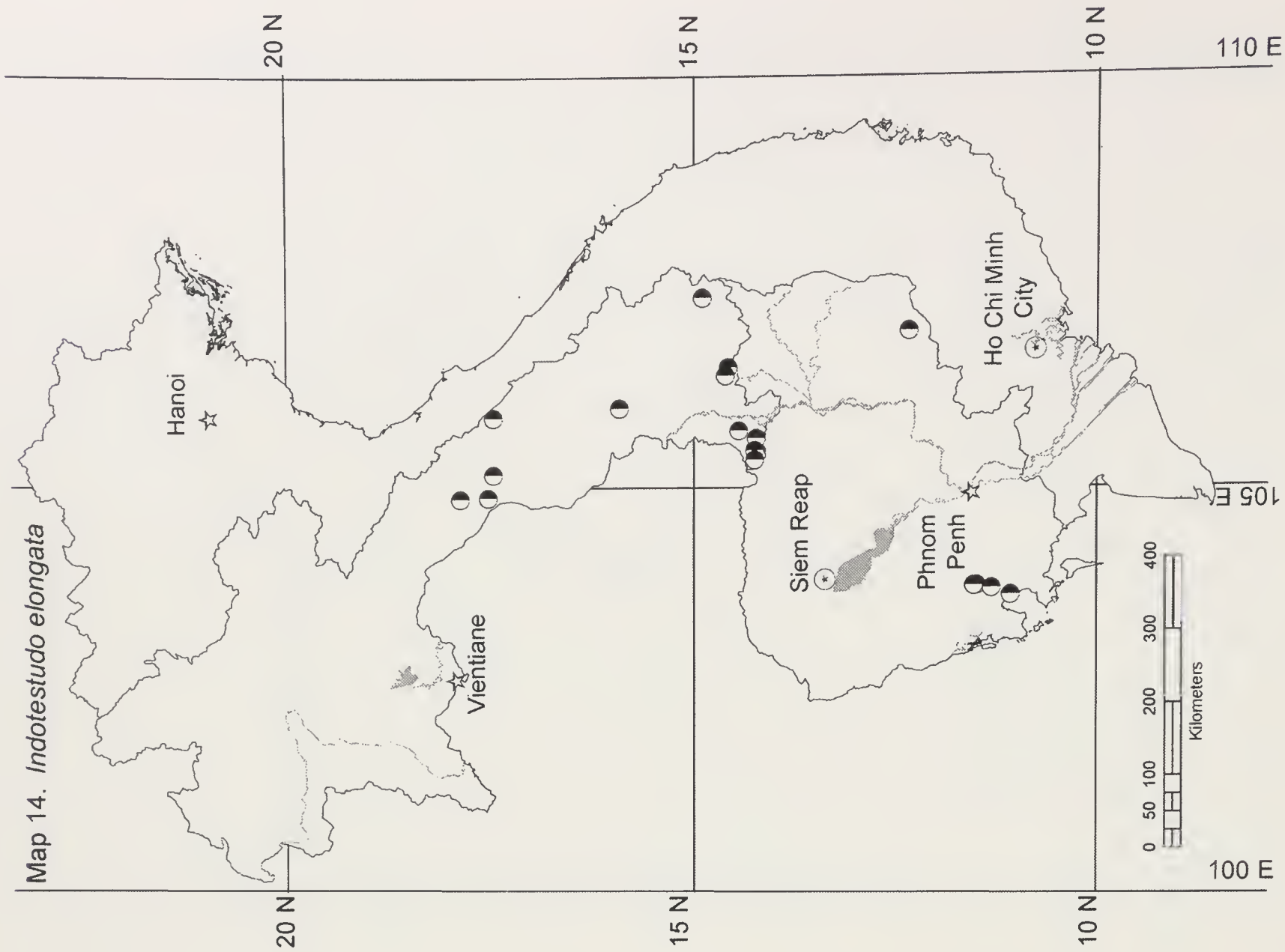


Map 9. *Heosemys grandis*

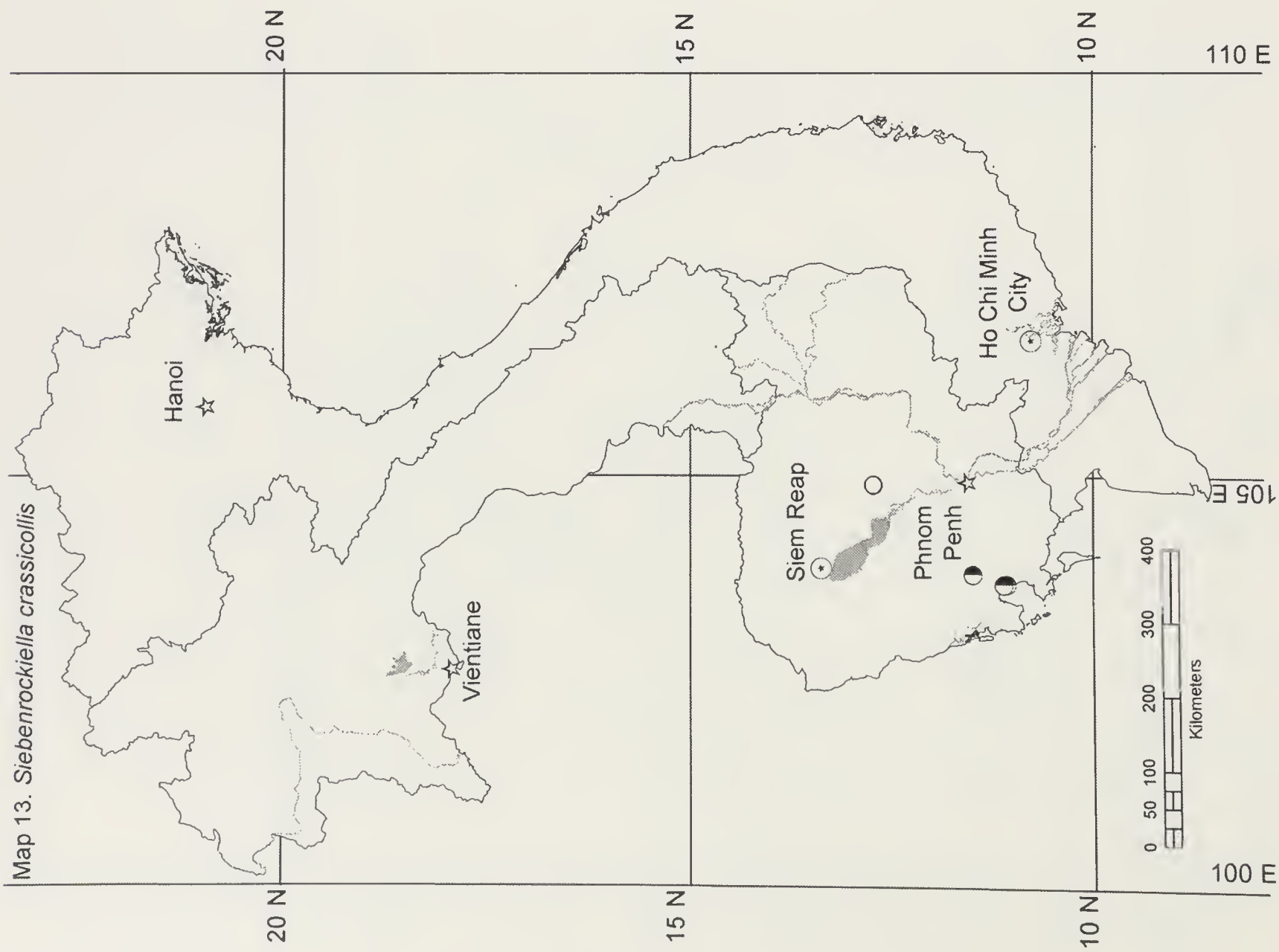


Map 12. *Sacalia quadriocellata*

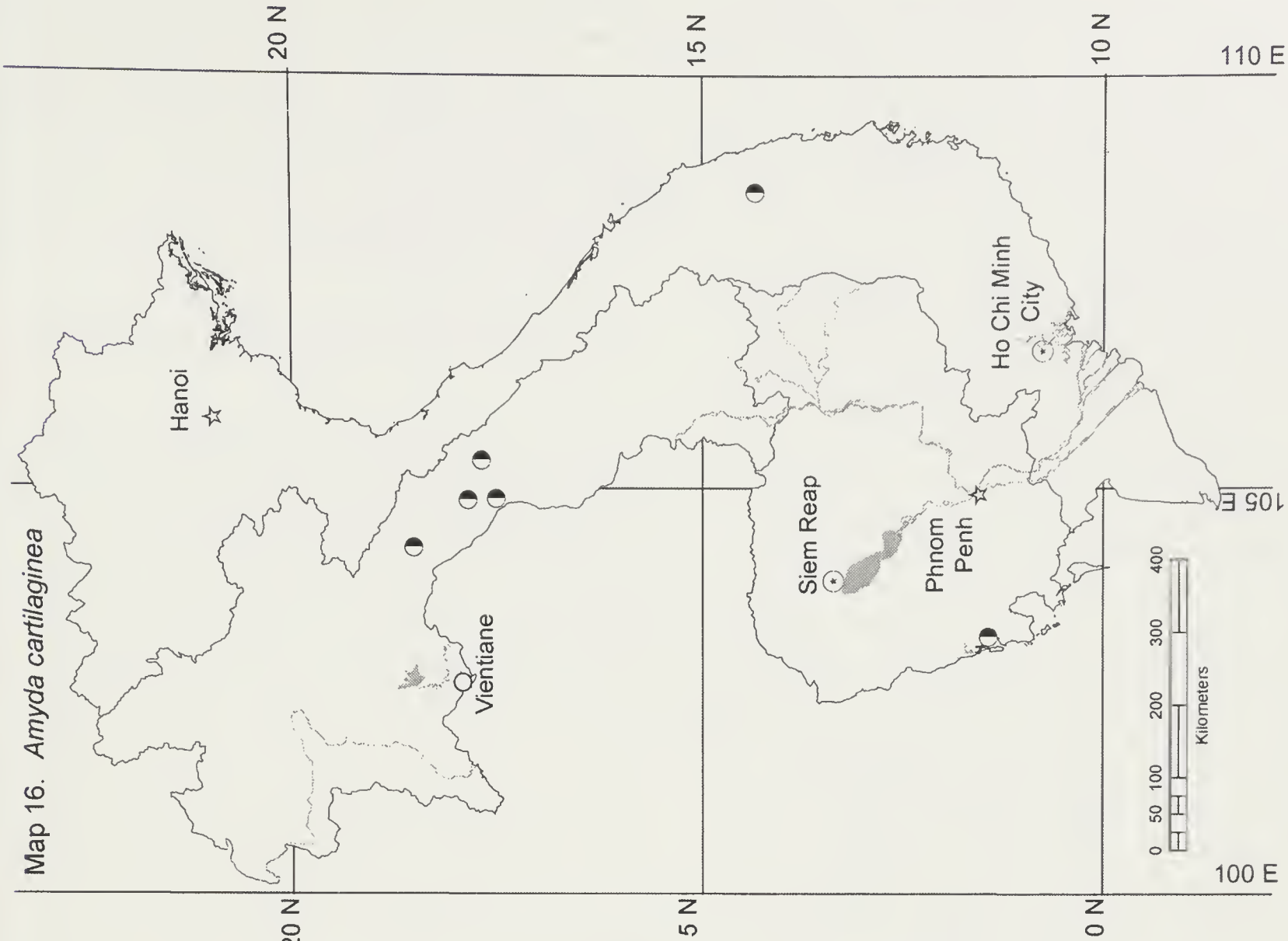
Map 11. *Malayemys subtrijuga*



Map 14. *Indotestudo elongata*

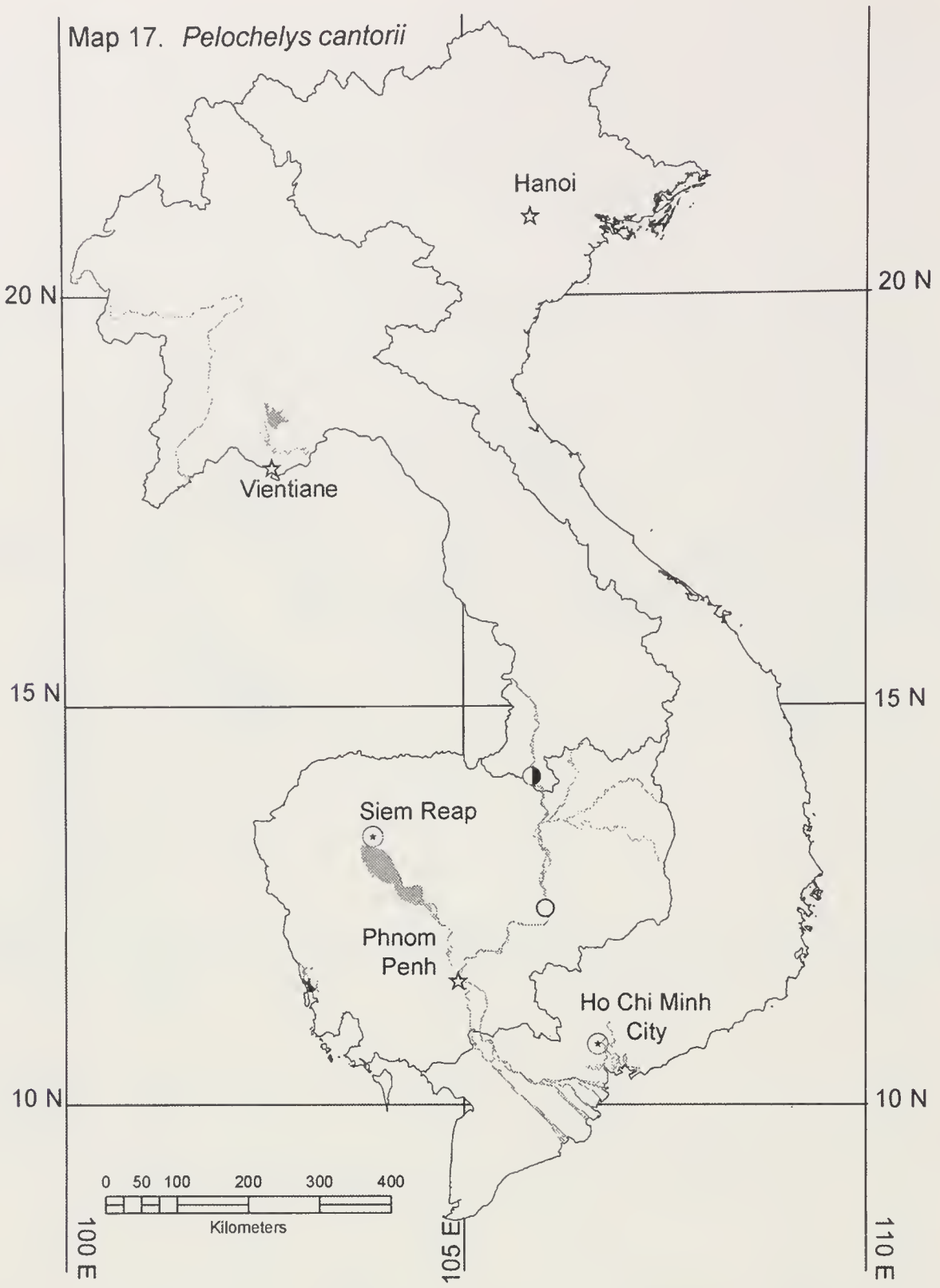


Map 13. *Siebenrockiella crassicollis*



Map 16. *Amyda cartilaginea*

Map 15. *Manouria impressa*



Maps 1-17 of records given in the text: shaded circles represent records collected in the field; half-shaded circles represent records obtained from hunters, abandoned hunting camps, or villages; unshaded circles represent records purchased from markets.

Hieremys annandalii (Boulenger, 1903)
[Map 10]

Cambodia. - **FMNH 259408**, carapace only, CL = 32.3, CW = 24.8, Phnom Penh, Oreussay Market, purchased in market, 17 May 1999, S. G. Platt. **FMNH 258876**, carapace and plastron, CL = 40.3, CW = 26.9, PL = 35.5, Battambang Province, Ek Phnom District, Koh Chivang Commune, Prek Toal Village on Tonle Sap Lake, 13° 14' 28" N 103° 39' 32" E, <10 m, eaten by residents of Prek Toal who captured it from nearby flooded forest, 27 August 1999, B. L. Stuart, J. Smith, K. Davey. **Fig. 12**, photograph only, same collecting information as FMNH 258876 except not yet eaten. **FMNH 259398**, carapace only, CL = 37.4, CW = 26.7, Siem Reap Province, Siem Reap District, Choeng Khneas Port on Tonle Sap Lake, found in fisherman's house, 28 June 2000, B. L. Stuart and S. G. Platt. **Fig. 13**, photograph only, two living animals, CL = 42.1 and PL = 34.7, CL = 33.4 and PL = 28.2, Siem Reap Province, Siem Reap District, Choeng Khneas Village, 13° 15.18' N; 103° 49.37' E, collected by residents of Choeng Khneas from Tonle Sap, 4 October 2000, S. G. Platt, Heng Sovannara, Long Kheng, and Vuthy Monyrath. **Fig. 14**, photograph only, CL = 37.2, PL = 28.4, Kampong Thom Province, Kampong Thom Town, 12° 42.69' N; 104° 53.31' E, photographed in market, 21 June 2000, S. G. Platt, Heng Sovannara, and Long Kheng.

Laos. - **FMNH 258879**, carapace and plastron only, CL = 33.3, CW = 23.0, PL = 31.3, Attapu Province, Sanamsai District, Xe Pian River Basin, Ban Chanto Village, 100-150 m, eaten by residents of Ban Chanto, 21 April 1995, T. D. Evans. **FMNH 259399**, carapace only, CL = 29.7, CW = 22.0, Attapu Province, Sanamxai

District, Ban Mai Village, 14° 42' 30" E 106° 29' 50" E, obtained from hunter in Ban Mai, 18 September 2000, B. L. Stuart and S. G. Platt.
Vietnam. - **FMNH 259074**, complete specimen, CL = 12.4, CW = 10.8, PL = 11.5, BD = 5.6, Kien Giang Province, An Minh District, Dong Hoa Town, 09° 45' 25" N 105° 00' 03" E, <10m, purchased from a reptile trade shop, 10 November 2000, B. L. Stuart.

Malayemys subtrijuga (Schlegel and Müller, 1844)
[Map 11]

Cambodia. - **FMNH 259404**, carapace only, CL = 19.2, CW = 14.1, Phnom Penh, purchased in market, 07 July 2000, S. G. Platt. **FMNH 259403**, carapace only, CL = 21.5, CW = 16.9, Siem Reap Province, Siem Reap District, Siem Reap Town, purchased from turtle restaurant, 11 December 1999, S. G. Platt. **Fig. 15**, photograph only, Battambang Province, Ek Phnom District, Koh Chivang Commune, Prek Toal Village on Tonle Sap Lake, 13° 14' 28" N 103° 39' 32" E, captured by residents of Prek Toal, 27 August 1999, B. L. Stuart, J. Smith, K. Davey. **FMNH 259402**, plastron only, PL = 17.8, collecting information same as FMNH 259403. **FMNH 259401**, carapace (broken) and plastron, CL = 23.2, PL = 20.0, Kampong Thom Province, Kampong Thom Town, obtained from restaurant, 22 June 2000, S. G. Platt. **Fig. 16**, photograph only, CL = 21.3, PL = 17.5, Kampong Thom Province, Sary Village, 12° 48.48' N 104° 44.19' E, collected by residents of Sary in Tonle Sap, 21 June 2000, S. G. Platt, Heng Sovannara, and Long Kheng. **Fig. 17**, photograph only, CL = 19.8, PL = 16.6, Kandal Province, Bassac Marshes, Prasat Village, 11° 17.72' N, 105° 08.61' E, captured by residents of Prasat, 5 July 2000, S. G. Platt, Heng Sovannara, and Long Kheng. **FMNH 259400**, plastron only, PL = 12.6, Koh Kong Province, Sre Ambel District, Chay Reap Village, west bank of Sre Ambel River, 11° 29' 10" N 103° 47' 00" E, <10 m, obtained from hunter in Chay Reap, 23° August 2000, B. L. Stuart and S. G. Platt.
Laos. - **Fig. 18**, photograph only, Vientiane Municipality, Vientiane, crossing road near culvert, May 1999, W. G. Robichaud. **FMNH 258868**, complete specimen, CL = 8.4, CW = 6.9, PL = 7.3, BD = 3.6, Vientiane Municipality, Vientiane, purchased in That Luang Fresh Food Market, 27 February 2000, B. L. Stuart. **FMNH 255269**, carapace only, CL = 15.9, CW = 12.9, Khammouan Province, Yommalat District, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban Vieng Village, 17° 20' N, 104° 57' E, eaten by residents of Ban Vieng, 30 March 1998, B. L. Stuart. **FMNH 258888**, plastron only, PL = 12.8, Khammouan Province, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban Chocksavang Village, eaten by residents of Ban Chocksavang, 22 May 1994, R. J. Timmins. **FMNH 259653** plastron (broken) only, collecting information same as FMNH 258888. **FMNH 259654**, plastron only, PL = 12.5, collecting information same as FMNH 258888. **FMNH 255268**, intact shell, CL = 10.9, CW = 8.8, PL = 9.2, BD = 4.8, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, Ban Thahin Village, on Xe Lepou River, 14° 08' N 105° 35' E, 60 m, eaten by residents of Ban Thahin, 17 July 1998, B. L. Stuart. **FMNH 255267**, complete specimen, CL = 10.9, CW = 8.4, PL = 9.3, BD = 4.7, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, Ban Tap Seng Village, 14° 15' N 105° 41' E, mixed deciduous forest, captured by resident of Ban Tap Seng for food, 25 July 1998, B. L. Stuart.
Vietnam. - **FMNH 259075**, complete specimen, CL = 5.3, CW = 4.3, PL = 4.4, BD = 2.7, Kien Giang Province, Vinh Thuang District, U Minh Thuong Nature Reserve, 09° 32' 40" N 105° 05' 11" E, <10m, flooded grassland and agricultural fields, caught in fishing net set in canal, 02 November 2000, B. L. Stuart. **FMNH 259394**, complete specimen, CL = 4.8, CW = 3.8, PL = 3.9, BD = 2.4, Kien Giang Province, An Minh District, U Minh Thuong Nature Reserve, 09° 37' 29" N 105° 07' 59" E, <10m, flooded grassland and agricultural fields, taken in fishing net, 16 November 2000, B. L. Stuart.

Sacalia quadriocellata (Siebenrock, 1903)
[Map 12]

Laos. - **FMNH 255270**, carapace only, CL = 13.8, CW = 10.6, Huaphahn Province, Vieng Tong District, Nam Et National Biodiversity Conservation Area, Nam Peun River, 20° 17' N 103° 25' E, 985 m, found in hunter's camp, 01 April 1998, P. Davidson. **FMNH 256542**, complete specimen, CL = 14.2, CW = 10.3, PL =12.5, BD = 4.5, Khammouan Province, Nakai District, Nakai-Nam Theun National Biodiversity Conservation Area, Annamite Mountains, 17° 50' N 105° 35' E, 600 m, wet evergreen forest along Houay Dreng Stream, found 1 m deep in pool with sandy substrate, 01 December 1999, B. L. Stuart. **FMNH 256543**, complete specimen, CL = 7.2, CW = 6.7, PL = 5.9, BD = 2.8, Khammouan Province, Nakai District, Nakai-Nam Theun National Biodiversity Conservation Area, Annamite Mountains, 17° 56' N 105° 31' E, 600 m, Houay Maka-Noi Stream near Ban Maka Village, collected by resident of Ban Maka, 15 November 1999, B. L. Stuart.

Remarks. - Ziegler (2002) field-collected and reported the species in local trade in Ha Tinh Province, Vietnam.

Siebenrockiella crassicollis (Gray, 1831)
[Map 13]

Cambodia. - **FMNH 259054**, complete specimen, CL = 14.3, CW = 10.5, PL = 11.7, BD = 5.8, Khampong Thom Province, Khampong Thom Town, 12° 42' N 104° 53' E, purchased from turtle trader in Khampong Thom Town, 21 June 2000, S. G. Platt. **FMNH 259053**, whole specimen, CL = 15.9, CW = 12.0, PL =13.7, BD = 6.8, Koh Kong Province, Sre Ambel District, Chay Reap Village, west bank of Sre Ambel River, 11° 29' 10" N 103° 47' 00" E, <10 m, captured by residents of Chay Reap, 24 August 2000, B. L. Stuart and S. G. Platt. **FMNH 259396,** intact shell, CL = 16.4, CW = 12.1, PL = 13.7, BD = 6.6, Koh Kong Province, Sre Ambel District, Chay Reap Village, west bank of Sre Ambel River, 11° 29' 10" N, 103° 47' 00" E, <10 m, obtained from hunter in Chay Reap, 24 August 2000, B. L. Stuart and S. G. Platt. **FMNH 259397**, plastron only, PL = 16.1, Koh Kong Province, Sre Ambel District, Kohriem Village on Sre Ambel River, obtained from hunter in Kohriem, 27 August 2000, B. L. Stuart and S. G. Platt. **FMNH 259055**, complete specimen, CL = 16.2, CW = 11.5, PL = 12.8, BD = 5.9, Koh Kong Province, Sre Ambel District, Prek Kroch River (tributary of Sre Ambel River), 11° 06' 20" N, 103° 39' 35" E, <10 m, flooded paddy at edge of mangrove and *Melaleuca* forest, captured by fisherman in bamboo fish trap set at that location, 27 August 2000, B. L. Stuart and S. G. Platt.

Remarks. - FMNH 259053 has a pale streak extending from the ear to the lower jaw, but the heads of FMNH 259054-55 are entirely dark, with no pale markings.

Testudinidae

Indotestudo elongata (Blyth, 1853)
[Map 14]

Cambodia: **FMNH 262316**, carapace only, CL = 14.7, CW = 10.0, Mondolkiri Province, Keo S'Marr District, Samling Logging Concession, 200 m, mixed deciduous forest and grassland, found in hunter's camp, 13 May 2000, J. Walston. **FMNH 262315**, plastron only, PL = 19.8, Koh Kong Province, Sre Ambel District, Chay Reap Village, west bank of Sre Ambel River, 11° 29' 10" N, 103° 47' 00" E, <10 m, obtained from hunter in Chay Reap, 23 August 2000, B. L. Stuart and S. G. Platt. **TC001** (held in the Field Museum of Natural History, Division of Amphibians & Reptiles), blood sample only, collecting information same as FMNH 262315, obtained from hunter in Chay Reap and released after taking blood sample, 23 August 2000, B. L. Stuart and S. G. Platt. **FMNH 262312**, plastron only, PL = 18.2, collecting information same as FMNH 262315. **FMNH 262307**, carapace only, CL = 25.6, CW = 15.1, collecting information same as FMNH 262315. **FMNH 262297**, carapace only, CL = 24.7, CW = 14.6, Koh Kong Province, Sre Ambel District, Boeung Tradok Pong Village, 11° 31' 10" N, 103° 46' 55" E, obtained from hunter in Boeung Tradok Pong, 24 August 2000, B. L. Stuart and S. G. Platt. **FMNH 262313**, plastron only, PL = 19.4, collecting information same as FMNH 262297. **FMNH 262314**, plastron only, PL = 18.2, collecting information same as FMNH 262297. **FMNH 262302**, carapace and plastron, CL = 19.5, CW = 13.0, PL = 16.5, Koh Kong Province, Sre Ambel District, Kohriem Village on Sre Ambel River, obtained from hunter in Kohriem, 27 August 2000, B. L. Stuart and S. G. Platt. **FMNH 262311**, plastron only, PL = 15.4, Koh Kong Province, Sre Ambel District, Chaouethail Plous Village on Sre Ambel River, 11° 18' 03" N, 103° 44' 56" E, obtained from hunter in Chaouethail Plous, 21 August 2000, B. L. Stuart and S. G. Platt. **FMNH 262310**, plastron only, PL = 14.8, collecting information same as FMNH 262311.

Laos. - **FMNH 262294**, carapace only, CL = 22.8, CW = 14.0, Khammouan Province, Boualapha District, Hin Nam No National Biodiversity Conservation Area, Ban Tasang Village, eaten by residents of Ban Tasang, 30 December 1995, R. J. Timmins. **FMNH 259056**, complete specimen, CL = 17.0, CW = 10.9, PL = 14.8, BD = 7.4, Khammouan Province, Nakai District, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban Na Bon Village, limestone karst with dry evergreen/mixed deciduous forest, 17° 54' N 104° 51' E, captured by residents of Ban Na Bon for food, 22 March 1998, B. L. Stuart and T. Chan-ard. **FMNH 262304**, carapace only, CL = 17.9, CW = 12.4, Khammouan Province, Thakhek District, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban Na Village, 17° 33' N, 104° 52' E, eaten by residents of Ban Na, 02 April 1998, B. L. Stuart. **FMNH 262299**, carapace only, CL = 24.2, CW = 15.4, Khammouan Province, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, Ban Namphick Village, eaten by residents of Ban Namphick, 22 May 1994, R. J. Timmins. **FMNH 262295**, carapace only, CL = 25.2, CW = 15.1, collecting information same as FMNH 262299. **FMNH 262296**, carapace only, CL = 26.9, CW = 16.7, Salavan Province, Xe Bang Nouan National Biodiversity Conservation Area, Ban Konglur Village, eaten by residents of Ban Konglur, 10 June 1994, R. J. Timmins. **FMNH 262301**, carapace only, CL = 29.0, CW = 18.1, Attapu Province, Xe Nam Noy River, Ban Mun Houa Muang Village, 300 m, eaten by residents of Ban Mun Houa Muang, April 1995, D. Showler. **FMNH 262303**,

Figure 28. See text for locality details and circumstances of the record. *Pelochelys cantorii* Champasak Province, Laos (photo I. G. Baird).

carapace only, CL = 23.3, CW = 14.4, Attapu Province, Sanamsai District, Xe Kong River, near Ban Sompoy Village and Cambodian border, 90 m, discarded carapace found in camp after being eaten by hunters, May 1995, T. D. Evans. **FMNH 262298**, carapace only, CL = 22.3, CW = 14.3, Champasak Province, Pathoumphon District, Xe Pian National Biodiversity Conservation Area, Xe Pian River upstream from Ban Phonsaat Village, 100 m, discarded carapace found in camp along Xe Pian River after being eaten by hunters, May 1995, T. D. Evans. **FMNH 262308,** carapace only, CL = 17.7, CW = 11.4, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, found in hunter's camp near Nong Sathevada Wetland, 14° 13' N 105° 36' E, 100 m, 04 March 1998, C. Francis. **FMNH 262306**, carapace only, CL = 18.9, CW = 12.0, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, Ban Baw Village, 14° 14' N, 105° 27' E, eaten by residents of Ban Baw, 18 July 1998, B. L. Stuart. **FMNH 262305**, carapace only, CL = 26.6, CW = 15.9, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, Ban Khiem Village, 14° 14' N, 105° 20' E, eaten by residents of Ban Khiem, 24 July 1998, B. L. Stuart. **FMNH 262300**, carapace only, CL = 24.9, CW = 14.7, Champasak Province, Mounlapamok District, Dong Khanthung Proposed National Biodiversity Conservation Area, Ban Kadian Village, 14° 26' N, 105° 42' E, eaten by residents of Ban Kadian, 29 July 1998, B. L. Stuart.

Remarks. - Ziegler (2002) reported the species in local trade in Ha Tinh Province, Vietnam.

Manouria impressa (Günther, 1882)
[Map 15]

Cambodia. - **Fig. 19**, photograph only of two intact shells, CL = 26.6 and PL = 23.8, CL = 22.8 and PL = 19.9, Koh Kong Province, Thmor Andart Village, along Stoeng Metoek River, 11° 49.23' N, 102° 53.62' E, collected by residents of Thmor Andart, 10 May 2001, S. G. Platt, Heng Sovannara, and Long Kheng. **Fig. 20**, photograph only, Ratanakiri Province, Oyadao District, found in house of Vietnamese wildlife trader on Cambodian side of Oyadao border checkpoint, Suon Phalla/TRAFFIC, 16 June 2002.
Laos. - **FMNH 262321**, carapace only, CL = 23.7, CW = 17.3, Phongsaly Province, Phongsaly District, Phou Dendin National Biodiversity Conservation Area, Ban Sopkang Village, 22° 05' 51" N, 102° 15' 02" E, eaten by residents of Ban Sopkang, 17 October 1999, B. L. Stuart and H. F. Heatwole. **FMNH 262317**, carapace only, CL = 27.7, CW = 19.9, collecting information same as FMNH 262321. **FMNH 262324**, carapace only, CL = 28.6, CW = 20.2, Huaphahn Province, Vieng Tong District, Phou Louey National Biodiversity Conservation Area, Ban Sa Kok Village, 20° 11" N, 103° 12" E, eaten by residents of Ban Sa Kok, 30 April 1998, B. L. Stuart. **FMNH 262319**, carapace only, CL = 27.0, CW = 19.9, collecting information same as FMNH 262324. **FMNH 262323**, carapace and plastron, CL = 20.8, CW = 16.3, PL = 19.4, collecting information same as FMNH 26234. **FMNH 262318**, carapace only, CL = 25.0, CW = 19.2, Huaphahn Province, Vieng Tong District, Phou Louey National Biodiversity Conservation Area, Ban Phone Xong Village, eaten by residents of Ban Phone Xong, 04 May 1998, D. Showler. **FMNH 262322**, plastron only, PL = 21.1, Khammouan Province, Hin Nam No National Biodiversity Conservation Area, Ban Katok Village, eaten by residents of Ban Katok, 12 January 1996, R. J. Timmins. **Fig. 21**, photograph only, Xe Kong Province, Kaleum District, Ban Talouy-Ngai Village, 15° 59' 50" N, 106° 57' 22" E, captured by residents of Ban Talouy-Ngai, 27 June 1999, B. L. Stuart. **FMNH 262320**, carapace only, CL = 27.6, CW = 20.6, Attapu Province, Xe Nam Noy River, Ban Taot Village, 800 m, eaten by residents of Ban Taot, April 1995, D. Showler.

Remarks. - Lehr and Holloway (2000) obtained a single carapace of *M. impressa* from a hunter in Ratanakiri Province, Cambodia, who claimed to have captured the turtle in mountains north of Siem Pang, Stung Treng Province.

Cheloniidae

Chelonia mydas (Linnaeus, 1758)

Cambodia. - **Fig. 22**, photograph only, Kampong Speu Province, Phnom Srouch District, Srei Khlong Market, 07 June 2000, B. L. Stuart.

Eretmochelys imbricata (Linnaeus, 1766)

Cambodia. - **Fig. 23**, photograph only, Sihanoukville Province, Mitta Pheap District, Koh Rong Island, Bagnu Village, obtained from fisherman in Bagnu, 01 January 2000, F. Goes.

Dermochelyidae

Dermochelys coriacea (Vandelli, 1761)

Cambodia. - **Fig. 24**, photograph only. Stuart et al. (2002) discussed in detail this record from offshore of the southern point of Koh Sra Mauch Island in the Gulf of Thailand, near Sihanoukville.

Trionychidae

Amyda cartilaginea (Boddaert, 1770)
[Map 16]

Cambodia. - **Fig. 25**, photograph only, CL = 7.4, Koh Kong Province, Koh Kong Knong Village, 11° 25.97' N; 103° 09.77' E, captured locally by villager in Stoeng Kep River, 11 May 2001, S. G. Platt, Heng Sovannara, and Long Kheng.
Laos. - **FMNH 258869**, complete specimen, CL = 7.4, CW = 6.8, PL = 2.1, BD = 5.7, Vientiane Municipality, Vientiane, purchased in That Luang Fresh Food Market, 27 February 2000, B. L. Stuart. **FMNH 258874**, complete specimen, CL = 29.5, CW = 26.0, PL = 20.6, BD = 9.5, Bolikhamxay Province, Northern Extension Proposed National Biodiversity Conservation Area, Ban Chom-Tong Village, near Nam Mouan River, captured by hunters in Nam Mouan River, 18 March 1995, R. J. Timmins. **Fig. 26**, photograph only, Khammouan Province, Nakai District, Nakai-Nam Theun National Biodiversity Conservation Area, Ban Kao-Oy Village, 17° 43' 39" N 105° 20' 05" E, captured by resident of Ban Kao-Oy, 03 November 1998, B. L. Stuart. **FMNH 255264**, complete specimen, CL = 18.2, CW = 16.4, PL = 13.8, BD = 4.5, Khammouan Province, Thakhek District, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, 17° 33' N, 104° 52' E, obtained from villager who captured it while fishing, 01 April 1998, B. L. Stuart. **FMNH 255265**, complete specimen, CL = 18.7, CW = 16.7, PL = 15.2, BD = 4.9, Khammouan Province, Nakai District, Khammouan Limestone (= Phou Hin Poun) National Biodiversity Conservation Area, 17° 54' N, 104° 51' E, obtained from villager who caught it in the Nam Thon River, 28 March 1998, B. L. Stuart.
Vietnam. - **FMNH 252163**, whole specimen, CL = 12.5, CW = 10.7, PL = 10.4, BD = 3.8, Gia-Lai Province, Ankhe District, Buon Loi Village, 20 km northwest of Kannack Town, Annamite Mountains, 14° 20' N, 108° 36' E, 700-750 m, Daklest River in the village, 07 May 1995, I. Darevsky and N. L. Orlov.

Remarks. - Farkas and Ziegler (2002) reviewed records of *A. cartilaginea* from Vietnam, Laos, and Cambodia.

Pelochelys cantorii Gray, 1864
[Map 17]

Cambodia. - **Fig. 27**, photograph only, Kratie Province, Kratie District, Kratie Town, purchased from fisherman in a Kratie market and released in the Mekong River after being photographed, September 2000, D. Gambade.
Laos. - **Fig. 28**, photograph only, Champasak Province, Khong District, Ban Hang Khone Village, captured by residents of Ban Hang Khone in the Mekong River, I. G. Baird.

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Studies on Pakistan Lizards: *Cyrtopodion stoliczkai* (Steindachner, 1867) (Gekkonidae: Gekkoninae)

KURT AUFFENBERG[1,*], KENNETH L. KRYSKO[2], AND WALTER AUFFENBERG[†]

[1]*Florida Museum of Natural History, Powell Hall,*
P. O. Box 112710, University of Florida, Gainesville, FL 32611 USA
**E-mail: kauffe@flmnh.ufl.edu*

[2]*Florida Museum of Natural History, Division of Herpetology,*
P. O. Box 117800, University of Florida, Gainesville, FL 32611 USA

[†]*(1928-2004)*

Abstract. - *Cyrtopodion stoliczkai* (Steindachner, 1867) is diagnosed based on the examination of 44 morphological characters in a series of 25 specimens collected near Skardu, Federally Administered Northern Areas (FANA), Pakistan. Observations on geographic distribution, habitat, and reproduction are provided. The questionable taxonomic status of *Gymnodactylus yarkandensis* Anderson, 1872 is discussed. *Alsophylax* (*Altiphylax*) *boehmei* Szczerbak, 1991 is regarded as a junior synonym of *C. stoliczkai.*

Key words. - *Cyrtopodion stoliczkai*, *Cyrtopodion yarkandensis*, *Alsophylax (Altiphylax) boehmei*, gecko, lizard, taxonomy, Pakistan.

Introduction

The diverse gecko fauna of Pakistan is poorly understood. Particularly problematic are the angular-toed or thin-toed geckos variously assigned to *Cyrtodactylus*, *Cyrtopodion*, and *Tenuidactylus*. Much of the taxonomic confusion stems from a general dearth of adequate material. Large series of specimens from which to identify variation in important taxonomic characters are lacking in most cases. Examination of specimens collected during surveys by Walter Auffenberg and the Zoological Survey Department of Pakistan in the 1980s-1990s provide insights to many questions regarding some of these poorly defined taxa. One such species, *Cyrtopodion stoliczkai* (Steindachner, 1867), is discussed below. Future contributions will examine additional species.

Materials and Methods

Herpetological collections were made in the vicinity of Skardu, Federally Administered Northern Areas (FANA), Pakistan in late August 1991. A series (n = 25) of *Cyrtopodion stoliczkai* comprised of all size classes ranging from newborns to adults was collected from under slabs of caliche broken off the edge of a dry creek bed near the Skardu Airport, ca. 10 km west of Skardu. These specimens were subsequently deposited in the Florida Museum of Natural History, University of Florida (UF 81327 - 81351).

This entire series was examined for 44 morphological characters (Tables 1 and 2). Although most of these counts and measurements are standard, clarification on certain characters are provided. Only original (not regenerated) tails were measured. The left side is given first for scale counts taken on both sides of the specimen. Character 6 was obtained by counting the scales surrounding five randomly selected enlarged dorsal tubercles. Character 12 lists color bands in the following order: occipital region, nape, body (from forelimbs to sacrum), and original tail. Character 13 lists the left side only for the number of scales between the eye and ear. The numbers of longitudinal rows of enlarged dorsal tubercles (Character 14) and transverse rows of ventral scales (Character 15) were taken at mid-body.

Source acronyms follow Leviton et al. (1985): BMNH (British Museum of Natural History, London); MCZ (Museum of Comparative Zoology, Harvard University); NMW (Naturhistorisches Museum, Wien); UF (Florida Museum of Natural History, University of Florida); ZFMK (Zoologischen Forschungsinstitutes und Museums Alexander Koenig, Bonn); ZSI (Indian Museum, Zoological Survey of India, Calcutta); ZSMH (Zoologische Staatssammlung München).

Results

Table 2 illustrates the variation of 44 morphological characters examined in 25 *Cyrtopodion stoliczkai* from Skardu. We found that these characters overlap with those available for *Alsophylax* (*Altiphylax*) *boehmei* Szczerbak, 1991. Therefore, we believe that *A. boehmei* should be considered a junior synonym of *C. stoliczkai* (see Discussion).

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Figure 1. *Cyrtopodion stoliczkai* (Steindachner, 1867) - dorsal and ventral views of adult (UF 81349) and subadult specimen (UF 81334) similar in size to holotype of *Alsophylax* (*Altiphylax*) *boehmei* (Szczerbak, 1991); both specimens collected near Skardu Airport, ca. 10 km. west of Skardu, FANA, Pakistan.

Cyrtopodion stoliczkai (Steindachner, 1867)
[Fig. 1; Tables 1,2]

Diagnosis. - Medium-sized geckos (snout-vent length [SVL] of largest adult = 46.5 mm), tail slightly longer than body (longest tail = 53.4 mm), SVL/tail length, mean = 0.854, Standard Deviation [SD] = 0.0455 (n = 11); limbs moderate, hind limb extends to axilla, forelimb to near nostril; body and head somewhat dorsoventrally compressed. Head moderate (head length/SVL, mean = 0.267, SD = 0.0267, head width/head length, mean = 0.696, SD = 0.0370, head height/head width, mean = 0.593, SD = 0.0546), snout equal to or slightly longer than distance between eye and ear. Eye large (eye diameter/eye - nostril, mean = 0.704, SD = 0.0665); ear rounded to ovate, small, ear diameter/eye diameter, mean = 0.148, SD = 0.0463. Nostril bordered by rostral, first supralabial, and normally 3 postnasals, occasionally fused to form 2 postnasals or split into 4 scales, medial postnasal smaller than others; 1 - 2 medial scales between postnasals (lacking in one specimen), when 2 present, one is often much larger than the other. Dorsal head scales generally homogeneous in size and shape, slightly larger on snout; 17 - 20 interorbital scales; loreals often with small projections on posterior half of eye; rostral partially cleft; 9-11 supralabials (12 on right side of one specimen), 7 - 9 infralabials. Mental triangular, longer than broad. 3 pairs of postmentals (rarely 2), decreasing in size posteriorly, first pair in contact, with a broad suture; second pair rarely disproportionate in size; third pair often variable in size, may be substantially enlarged on one side, often separated from infralabials by a series of small scales. Dorsum of body and limbs with small roundish, beaded to flat scales intermixed with larger, roundish tubercles; tubercles surrounded by rosettes of 7 - 9 small scales, 2 - 3 times larger than granular scales, smooth, flat to rounded, sometimes indistinctly keeled, slightly conical laterally; arranged in 8 - 10 (rarely 12) longitudinal rows, lateral rows indistinct. Lateral fold indistinct, often absent. Venter with roundish, slightly imbricate scales, 25 - 31 across middle of belly; 113 - 135 from postmentals to cloaca. Preanal and femoral pores absent. Femoral spines absent. Cloacal spines present, 1 - 2 per side. Digits moderate, subdigital lamellae well-developed, nearly as broad as digit, 16 - 20 on fourth finger, 10 - 12 on first toe, 19 - 27 on fourth toe. Tail dorso-ventrally compressed on anterior two-thirds, round on posterior one-third; anterior half with dorsal medial groove; anterior half distinctly segmented, swollen and lobed laterally in adults, less so in subadults and juveniles, tapering to point; 5 whorls on anterior one-third on tail; each segment on anterior half with one enlarged dorso-lateral tubercle and 2 - 3 enlarged, bluntly conical lateral tubercles per side, medial tubercles largest; tubercles reduced in size and number (2) distally, indistinct or absent on posterior one-third; 6 - 7 rows of scales per whorl, terminal row not enlarged, squared-off posteriorly, not acuminate or keeled; 2 series of small subcaudals, cycloid, not greatly enlarged transversely, only about twice as large as adjacent scales, separated by medial groove on anterior half to two-thirds of tail; regenerated tail without segments and lobes, uniformly covered in small flattened scales.

Dorsal ground color light to medium gray with 7 - 10 irregular transverse darker gray bands, with even darker posterior margins; 1 on occipital area, 1 on nape, and 5 - 8 on body; 10 - 15 on tail; limbs with short grayish bands; grayish-brown band from nostril through eye; top of head irregularly mottled; labials with dark speckles; venter whitish.

Table 1. Morphological Characters examined for *Cyrtopodion stoliczkai* from Pakistan. See text for character descriptions.

1. Number of post-nasals
2. Number of medial scales between post-nasals
3. Number of supralabials
4. Number of infralabials
5. Number of interorbitals
6. Number of scales surrounding dorsal tubercle (randomly counted 5 tubercles)
7. Number of scales between postmentals and cloaca
8. Number subdigital lamellae on fourth toe
9. Number of pairs of postmentals
10. Number of whorls on anterior one-third of tail
11. Number of large, lateral tubercles on each tail whorl
12. Number of color bands on head, nape, body, and tail
13. Number of scales between eye and ear (left side only)
14. Number of longitudinal rows of tubercles
15. Number of transverse rows of ventral scales at mid-body
16. Number of subdigital lamellae on first toe
17. Presence (+) and number of cloacal spines
18. Number of scale rows per tail whorl (max. 8 whorls counted)
19. Number of subdigital lamallae on fourth finger
20. First pair of postmentals in contact (+) or not in contact (-)
21. Scales on top of head homogeneous in size (+) or not homogeneous in size (-)
22. Dorsal tubercles present (+) or absent (-)
23. Mental triangular (+) or not triangular (-)
24. Tail whorls distinct (+) or indistinct (-)
25. Preanal pores present (+) or absent (-)
26. Color pattern of dorsum banded (+) or not banded (-)
27. Color band from nostril through eye to nape present (+) or absent (-)
28. Femoral spines present (+) or absent (-)
29. Femoral pores present (+) or absent (-)
30. Enlarged tubercles on limbs present (+) or absent (-)
31. Roundish dorsal tubercles present (+) or absent (-)
32. Dorsal tubercle sculpture rounded (+) or not rounded (-)
33. Medial subcaudals in series (+) or not in series (-)
34. Distal scale row of tail whorl enlarged (+) or not enlarged (-)
35. Tail dorsoventrally compressed (+) or not compressed (-)
36. Snout-vent length (SVL)
37. Tail length
38. Head length
39. Head width
40. Head height
41. Nostril-eye distance
42. Eye-ear distance
43. Eye diameter
44. Ear diameter

Distribution. - *Cyrtopodion stoliczkai* has been recorded from various localities (see references cited herein) in the upper Indus River valley ranging from Leh, Kashmir to Skardu, Pakistan, a distance of almost 300 km by air (Fig. 2). This species was collected in the Kargil vicinity in Kashmir along one of the many tributaries of the upper Indus River and may occur in other associated river valleys as well. The Shyok River, a large tributary draining areas to the north of the Indus River, remains virtually unexplored. The Indus River enters a series of gorges west of Skardu, which may impede dispersal in that direction.

Habitat. - *Cyrtopodion stoliczkai* occurs in the Pamir-Karakorum Highlands region of northern Pakistan and adjacent Kashmir at elevations from 2300 to 3700 m. Vegetation is sparse in this region, being generally confined to human occupation sites, seeps, streams, and forested valleys. The intervening barren landscape is characterized by stark and steep mountainsides, rock and boulder fields, and large areas of clay, caliche, and sand. This species has not been collected from human habitations. Some individuals from the large series collected by Stoliczka during the Second Yarkand Expedition were found under stones (Blanford, 1878). Gruber (1981) collected most of his series in rocky habitats, although one specimen was found in a small hole in a willow tree. Our series was collected from small cracks and fissures between slabs of caliche (see above).

Reproduction. - In the vicinity of Skardu, hatching occurs in mid to late August. In addition to several newborns, three full-term eggs (UF 81352) were collected in a cavity between slabs of caliche on 29 August 1991. Although collected together, it is unknown if these represent a single clutch or communal oviposition site. Egg measurements range from 9.7 - 11.1 mm in length and 7.6 - 8.5 mm in width.

Discussion

The assignment of the species epithet "*stoliczkai*" to the genus *Cyrtopodion* Fitzinger, 1843 is arbitrary. The generic assignments of the angular-toed geckos of South and Central Asia have undergone a great deal of revision over the last few decades (see Anderson, 1999 for a synopsis of the nomenclature history). In this paper we follow the simplified arrangement presented by Anderson (1999) on Iranian species of this group, as we assign all Pakistan species of angular-toed geckos to the genus *Cyrtopodion*. We also find it prudent, considering the current taxonomic confusion, not to allocate subgenera. *Cyrtopodion stoliczkai* is presently not

Table 2. Measurements and scale counts for *Cyrtopodion stoliczkai* from Pakistan. See text and Table 1 for character descriptions. Note that all specimens residein the UF, except specimen with asterisk (= ZFMK).

Specimen	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
81327	3/3	1	10/9	7/8	19	7-8	135	23/22	3/3	NA	2	1/1/5/10	17	8	29	10/10	+/2/2	6-7	19/19	+	+
81328	3/3	1	10/10	7/7	20	7-9	125	22/23	3/3	5	2	1/1/5/12	17	8	30	11/11	+/2/2	6	18/17	+	+
81329	3/3	0	10/10	7/7	17	7-8	117	23/23	3/3	NA	2	1/1/5/10	17	8	29	10/11	+/2/2	6-7	19/19	+	+
81330	3/3	2	11/10	9/9	18	7-8	113	22/23	2/3	NA	2	1/1/5/NA	17	10	31	10/10	+/2/2	NA	18/18	+	+
81331	4/3	1	10/10	8/8	20	7-8	127	23/23	3/3	NA	2	1/1/5/13	16	10	31	11/11	+/2/2	6-7	18/18	+	+
81332	3/3	2	10/10	8/8	18	7-8	116	26/26	3/3	5	2	1/1/5/NA	16	10	27	12/12	+/2/2	6-7	18/18	+	+
81333	3/3	2	10/10	8/9	19	7-8	122	23/21	3/3	5	2	1/1/6/15	17	10	27	10/10	+/2/2	6-7	16/17	+	+
81334	3/3	1	10/10	7/7	18	7-8	119	22/23	3/3	5	2	1/1/6/11	16	8	28	10/10	+/2/2	6-7	19/19	+	+
81335	3/3	1	9/9	8/8	18	7-8	113	22/21	3/3	5	2	1/1/6/NA	17	12	28	10/10	+/2/2	6-7	19/18	+	+
81336	3/3	1	11/11	8/7	20	7-9	126	22/22	2/2	NA	2	1/1/6/NA	16	10	28	10/10	+/2/2	6-7	19/18	+	+
81337	3/3	2	10/10	8/7	20	8	126	23/22	3/3	5	2	1/1/6/15	17	8	25	11/11	+/2/2	6	18/18	+	+
81338	3/3	1	11/10	7/7	20	7-8	132	23/24	3/3	NA	2	1/1/6/NA	17	10	28	10/10	+/2/2	6-7	18/17	+	+
81339	3/3	1	10/10	7/8	20	7-8	118	20/20	3/3	NA	2	1/1/5/NA	17	8	26	10/10	+/1/1	6-7	18/19	+	+
81340	3/3	1	10/10	7/7	19	7-9	117	19/19	2/3	5	2	1/1/6/14	17	10	27	10/10	+/2/2	6	19/19	+	+
81341	3/3	2	11/11	8/8	20	8	124	22/20	3/3	5	2	1/1/5/NA	16	8	26	10/10	+/1/1	6	18/18	+	+
81342	2/2	2	10/11	8/8	17	7-8	116	22/23	3/3	NA	NA	1/1/6/NA	16	8	26	11/10	+/2/2	NA	18/18	+	+
81343	3/3	2	10/11	8/7	17	7-8	115	23/22	3/3	5	2	1/1/5/13	16	10	30	10/10	+/2/2	6-7	18/18	+	+
81344	2/2	1	10/10	7/7	18	7-9	129	23/22	3/3	5	2	1/1/6/NA	15	10	26	11/11	+/1/1	6-7	17/17	+	+
81345	3/3	2	10/10	9/9	17	7-8	119	24/26	3/3	5	2	1/1/6/13	16	8	28	10/11	+/2/2	6-7	18/19	+	+
81346	3/3	2	11/10	9/8	18	8-9	129	25/27	3/3	5	2	1/1/6/12	16	8	29	11/11	+/2/2	6	18/20	+	+
81347	3/3	1	10/10	8/8	18	7-8	115	-/24	3/3	NA	2	1/1/6/NA	17	8	27	NA/10	+/2/2	6-7	18/18	+	+
81348	3/3	1	9/9	8/8	20	7-9	114	23/23	3/3	NA	2	1/1/5/NA	16	8	25	11/11	+/2/2	6	18/18	+	+
81349	3/3	2	10/10	9/9	19	7-8	122	25/24	3/3	5	2	1/1/8/13	17	8	25	11/11	+/2/2	6-7	20/20	+	+
81350	3/3	1	10/10	7/7	18	7-9	130	26/24	3/3	NA	NA	1/1/7/NA	16	8	28	11/11	+/1/1	NA	20/19	+	+
81351	3/3	1	11/12	9/9	19	7-8	122	22/23	3/3	5	2	1/1/6/NA	16	8	29	11/11	+/2/2	6-7	18/18	+	+
38773*	3/3	1	9/9	6/7	20	8	NA	NA	3/3	NA	2	1/1/5/12	NA	NA	NA	NA	NA	NA	NA	+	+

Table 2. Continued.

Specimen	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
81327	+	+	-	-	+	+	-	-	+	+	+	+	-	+	23.7	25.0	6.8	4.6	2.6	1.9	1.9	1.4	0.1
81328	+	+	+	-	+	+	-	-	+	+	+	+	-	+	45.1	52.5	13.7	8.3	5.1	3.4	3.4	2.4	0.2
81329	+	+	-	-	+	+	-	-	+	+	+	+	-	+	20.1	17.5	7.5	4.4	2.7	1.6	1.6	1.3	0.1
81330	+	+	NA	-	+	+	-	-	+	+	+	+	-	+	43.6	NA	11.0	7.9	4.8	3.3	3.3	2.2	0.3
81331	+	+	-	-	+	+	-	-	+	+	+	+	-	+	34.0	41.0	9.2	6.1	3.6	2.7	2.4	1.8	0.2
81332	+	+	+	-	+	+	-	-	+	+	+	+	-	+	36.7	NA	9.5	6.9	4.2	3.0	3.0	2.1	0.3
81333	+	+	+	-	+	+	-	-	+	+	+	+	-	+	41.9	47.5	10.7	7.6	4.2	3.4	3.4	2.4	0.5
81334	+	+	+	-	+	+	-	-	+	+	+	+	-	+	33.4	41.5	8.5	6.0	3.3	2.5	2.5	1.7	0.3
81335	+	+	+	-	+	+	-	-	+	+	+	+	-	+	41.1	NA	10.6	7.6	4.5	3.3	3.3	2.2	0.3
81336	+	+	+	-	+	+	-	-	+	+	+	+	-	+	44.0	NA	11.3	8.1	4.8	3.4	3.0	2.5	0.4
81337	+	+	+	-	+	+	-	-	+	+	+	+	-	+	38.7	46.6	9.7	7.0	4.0	2.6	2.6	2.0	0.5
81338	+	+	+	-	+	+	-	-	+	+	+	+	-	+	37.9	NA	10.1	6.9	3.8	3.1	3.1	2.2	0.4
81339	+	+	+	-	+	+	-	-	+	+	+	+	-	+	22.0	NA	6.5	4.3	2.7	1.5	1.5	1.4	0.1
81340	+	+	+	-	+	+	-	-	+	+	+	+	-	+	36.3	46.3	9.8	6.6	5.2	2.9	2.5	2.0	0.3
81341	+	+	+	-	+	+	-	-	+	+	+	+	-	+	45.0	NA	11.3	8.0	4.8	3.6	3.6	2.6	0.3
81342	+	+	NA	-	+	+	-	-	+	+	+	+	-	+	34.1	NA	9.5	7.0	4.0	2.9	2.9	1.9	0.3
81343	+	+	+	-	+	+	-	-	+	+	+	+	-	+	41.5	48.8	10.9	7.6	5.4	3.6	3.6	2.4	0.4
81344	+	+	+	-	+	+	-	-	+	+	+	+	-	+	46.5	NA	11.3	8.2	4.6	3.5	3.5	2.2	0.4
81345	+	+	+	-	+	+	-	-	+	+	+	+	-	+	43.4	51.0	10.8	7.8	4.3	3.2	3.2	2.2	0.4
81346	+	+	+	-	+	+	-	-	+	+	+	+	-	+	43.5	48.1	11.1	8.1	4.6	3.5	3.5	2.3	0.4
81347	+	+	+	-	+	+	-	-	+	+	+	+	-	+	37.2	NA	9.4	6.3	3.8	2.8	2.8	2.0	0.2
81348	+	+	+	-	+	+	-	-	+	+	+	+	-	+	43.9	NA	11.1	7.8	4.2	3.5	3.5	2.2	0.4
81349	+	+	+	-	+	+	-	-	+	+	+	+	-	+	45.1	53.4	11.5	8.3	4.6	3.7	3.7	2.5	0.5
81350	+	+	NA	-	+	+	-	-	+	+	+	+	-	+	40.0	NA	10.5	7.3	4.1	3.0	3.0	2.3	0.4
81351	+	+	+	-	+	+	-	-	+	+	+	+	-	+	34.0	NA	9.1	6.5	3.7	2.8	2.8	1.7	0.2
38773*	+	+	-	-	+	+	NA	NA	NA	NA	NA	NA	NA	NA	34.6	35.7	NA	7.2	4.4	NA	NA	1.5	0.5

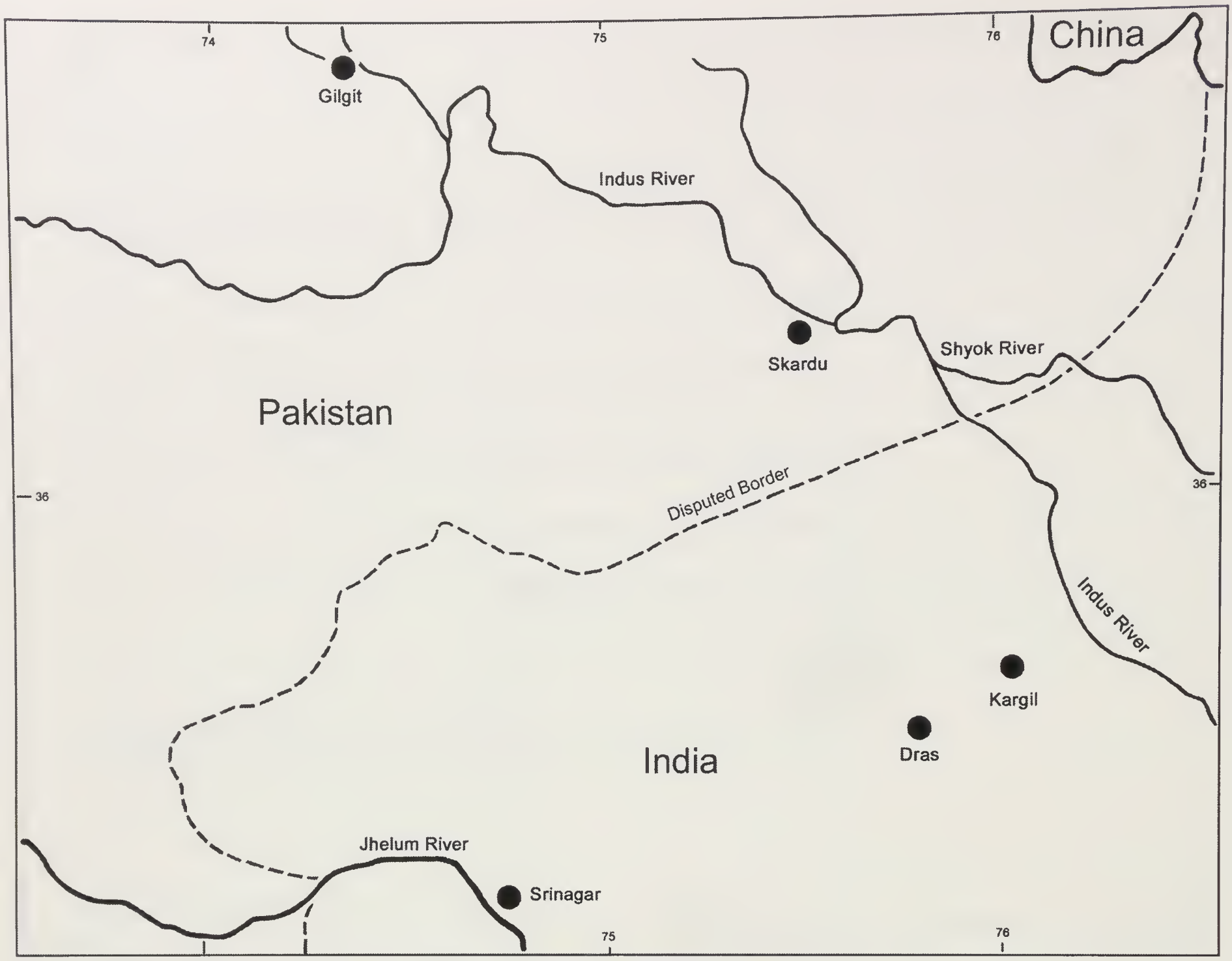

Figure 2. Map of reported localities of *Cyrtopodion stoliczkai* (Steindachner, 1867).

assigned to a subgenus, but is regarded as a member of the "Tibeto-Himalayan" group. Our somewhat cursory examination of other members of this group, including *C. baturensis* (Khan, 1992), *C. chitralensis* (Smith, 1935) (synonymized with *C. walli* (Ingoldby, 1922) by Khan, [1992]), and *C. mintoni* (Golubev and Szczerbak, 1981), clearly shows that this group is highly artificial.

Khan and Rosler (1999) did not consider *Cyrtopodion stoliczkai* as a member of the Pakistan gecko fauna, confining it to the upper Indus River valley in Kashmir. However, the morphological characters of our series from Skardu closely match those of Szczerbak and Golubev (1986, 1996) and Khan and Rosler (1999). Therefore, *C. stoliczkai* does indeed occur in Pakistan.

Cyrtopodion stoliczkai (Steindachner, 1867) was described from a single specimen collected by Ferdinand Stoliczka in 1865 near Karoo, north of Dras, in northern Kashmir (Blanford, 1878). Some previous authors have cited Steindachner (1869) as the original description, but this actually refers to a reprint of the earlier work (K. Adler, pers. comm.). This single specimen was subsequently transferred to the Naturhistorisches Museum, Wien (Vienna, Austria), where Steindachner designated it as the holotype (NMW 16756) in honor of its collector. The holotype is well-illustrated by Szczerbak and Golubev (1986, 1996:Fig. 92). During the Second Yarkand Expedition (1873 - 1874), Stoliczka collected an additional 46 specimens from the type locality and a few localities eastward to Leh in the Indus River valley of central Ladakh, Kashmir. These specimens were subsequently deposited in the Indian Museum, Calcutta (Blanford, 1878). Annandale (1913) enumerated only 31 specimens in the Indian Museum collections in his treatment of Indian *Gymnodactylus*. Zugmayer (1909) and Brongersma (1935) reported this species from Lamayuru and Leh, respectively, both localities being in central Ladakh. Gruber (1981) collected 14 specimens from a few localities in the same general area as Stoliczka in 1865, which were deposited in the ZSM. Khan and Rosler (1999) presented a detailed redescription of *C. stoliczkai* based on this last series, but were unable to examine the holotype and the series in the Indian Museum. Khan and Rosler (1999) erroneously referred to a specimen of *C. stoliczkai* in the

Museum of Comparative Zoology (MCZ 7132) as both a syntype and paratype. This specimen cannot be considered either, as Steindachner mentioned only one specimen in the original description, and Constable (1949:84) did not provide any type designation for this MCZ specimen. This specimen was received by the MCZ via exchange with the Indian Museum, Calcutta, in June 1908 (Constable, 1949:61; J. Rosado, pers. comm.). Stoliczka is given as the collector (Constable, 1949:61). Stoliczka died in 1874 during the Second Yarkand Expedition's return to India, indicating that his large series from Ladakh in the Indian Museum was collected in 1873 during the outbound portion of the expedition. We must assume that the MCZ specimen originates from this large series, however, it is possible that Stoliczka made additional collections in Ladakh between 1865 and 1873. Nevertheless, it is clear that Steindachner (1867) examined only one specimen at the time *C. stoliczkai* was described and the MCZ specimen cannot be a type. Additionally, Khan and Rosler (1999) referred to MCZ 7132 as a topotype. This may or may not be correct, as Stoliczka's journal from the Second Yarkand Expedition indicated that only some of his specimens were collected at the type locality (Blanford, 1878) and others were collected elsewhere. However, since the only locality information available for the MCZ specimen is "Ladakh", it cannot be ascertained that it is actually one of the specimens collected at the type locality.

Gymnodactylus walli Ingoldby, 1922 and *G. yarkandensis* Anderson, 1872 were regarded as synonyms of *Cyrtopodion stoliczkai* by Smith (1935), a view followed by virtually all subsequent authors. Minton (1966) referred to a single specimen from Udigram, Swat District, Northwest Frontier Province, Pakistan as *C. stoliczkai*, which was later found to be a distinct species (Mertens, 1969:26; Khan, 1980:14; described as *Gymnodactylus mintoni* by Golubev and Szczerbak in 1981). Khan (1992) produced a compelling argument to consider *Cyrtopodion walli* distinct from *C. stoliczkai* based on an examination of the type specimens in the British Musuem. We are unable to resolve the synonymy of *C. yarkandensis* (Anderson, 1872). Blanford (1878) relegated *C. yarkandensis* to the synonymy of *C. stoliczkai* (Steindachner, 1867), and subsequent authors followed this view (Annandale, 1913; Boulenger, 1890; Kluge, 1991, 1993, 2001; Mertens, 1969; Minton, 1966; Smith, 1935; Szczerbak and Golubev, 1986, 1996; Wermuth, 1965; Zhao and Adler, 1993). Khan (1994) resurrected *C. yarkandensis* based on an examination of a single specimen housed in the British Museum (BMNH 72.3.22.4). A comparison of color transparencies taken during a study of the same specimen by W. Auffenberg in the early 1990s, along with our series from Skardu, indicate that this specimen is probably best assigned to *C. stoliczkai*. However, important morphological characters cannot be ascertained from the transparencies or Khan's (1994) description. Szczerbak and Golubev (1986, 1996) also assigned this specimen to *C. stoliczkai*. Whether *C. yarkandensis* is a distinct taxon or a synonym of *C. stoliczkai* can be determined only with a thorough examination of the types housed in the Indian Museum, Calcutta. We provide the following notes on *C. yarkandensis* at this point merely for a historical perspective.

Anderson (1872) mentioned two specimens in his description of *Cyrtodactylus yarkandensis*. These were supposedly collected in Yarkand (= Shache, Xinjiang, China; Zhao and Adler, 1993) during the First Yarkand Expedition in 1870 (Blanford, 1878). This locality was doubted by Blanford (1878:12-13), maintaining that the types of *C. yarkandensis* were identical to the *C. stoliczkai* specimens collected by Stoliczka during the Second Yarkand Expedition in Ladakh, some of which were taken from the type locality of *C. stoliczkai*. Blanford (1878:13) stated "The specimens described by Dr. Anderson as *Cyrtodactylus yarkandensis* were brought, with others, by a collector, who accompanied Dr. Henderson on the mission which was sent to Yárkand in 1870; this mission traversed precisely the same route through Kashmir and Leh as the second in 1873 - 74, and I do not think there can be any reasonable doubt that the real locality whence *Cyrtodactylus yarkandensis* was obtained must have been Ladák, and not Yárkand." Annandale (1913:316) incorrectly attributed the collection of the types of *C. yarkandensis* to Stoliczka during the Second Yarkand Expedition. That mission embarked in 1873, about one year after Anderson's (1872) description of *C. yarkandensis*. Khan (1994) referred to this specimen (BMNH 72.3.22.4; "Yarkhand") as a syntype. The specimen catalogue at the British Museum indicates that this specimen was "Presented by [the] Indian Museum Calcutta through Dr. Anderson" and cataloged on March 22, 1872 (C. McCarthy, pers. comm.), the same year the species was described. Anderson (1872:381) mentioned only two specimens in the original description and Annandale (1913:316) referred to two specimens (ZSI 3792 - 93) as types of *C. yarkandensis* (as a synonym of *Gymnodactylus stoliczkai* Steindachner) in the Indian Museum, Calcutta. It can be assumed that these were the specimens on which Anderson based his description, thus the status of the British Museum specimen remains nebulous.

Alsophylax (*Altiphylax*) *boehmei* Szczerbak, 1991 was described from two specimens collected by G. Osella from Skardu, Pakistan in July 1976. Although we did not examine the holotype, we have no doubt that the description of this species is based on subadult

Cyrtopodion stoliczkai. This relationship was originally suggested by Golubev (in Szczerbak and Golubev, 1996:200, footnote). Morphological characters for *A. boehmei* provided by Szczerbak (1991) fall within the range of variation in those we recorded for *C. stoliczkai* (Table 1). The holotype (ZFMK 38773, see Fig. 3 in Szczerbak, 1991) matches the subadults in our complete growth series collected in Skardu in 1991 (Table 2). The whorls of the anterior third of the tail of *C. stoliczkai* do not become swollen and lobed until maturity, but Szczerbak (1991) lacked a sufficient series of specimens to make this determination.

Golubev (in Szczerbak and Golubev, 1996:200, footnote) also suggested that *Tenuidactylus baturensis* Khan and Baig, 1992 may also be conspecific with *Cyrtopodion stoliczkai*. Our examination of one specimen collected near the type locality of *T. baturensis* indicates that although it is similar in overall morphology, this species appears to be distinct.

Khan (2001) divided the Tibeto - Himalayan group of *Cyrtopodion* into three subgroups: Stoliczkai subgroup = *C. baturensis* (Khan and Baig, 1992), *C. stoliczkai* (Steindachner, 1867), and *C. yarkandensis* (Anderson, 1872); Tibetinus subgroup = *C. battalensis* (Khan, 1993), *C. dattanensis* (Khan, 1980), *C. himalayanus* (Duda and Sahi, 1978), *C. mintoni* (Golubev and Szczerbak, 1981), and *C. tibetinus* (Boulenger, 1905); and the Walli subgroup - *C. walli* (Ingoldby, 1922) (including *C. chitralensis* [Smith, 1935] as a synonym) and *C. kirmanense* (Nikolsky, 1900). Our preliminary examination of most of these taxa reveals that Khan's system has merit concerning overall morphological and ecological data. Further investigations into the Pakistan gecko fauna and that of adjacent areas will undoubtedly lead to further discoveries of new species and more clearly define those already described.

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Antimicrobial Activity in the Skin Secretion of *Bufo viridis* (Laurenti, 1768)

BAŞARAN DÜLGER[1,*], İSMAIL HAKKI UĞURTAŞ[2], AND MURAT SEVINÇ[2]

[1]*Canakkale Onsekiz Mart University, Faculty of Science & Arts, Department of Biology, Canakkale-Turkey*

[2]*Uludağ University, Faculty of Science & Arts, Department of Biology, Bursa-Turkey*

[*]*Correspondence author, E-mail: dbasaran@comu.edu.tr; Fax number: +90.286.2180533*

Abstract. - In this study, antimicrobial activity of various extracts prepared from *Bufo viridis* skin secretion were tested against the microorganisms by disk diffusion method. *Escherichia coli* ATTC 10536, *Listeria monocytogenes* ATCC 19117, *Klebsiella pneumoniae* UC57, *Salmonella typhi* ATCC 19430, *Staphylococcus aureus* ATCC 6538P, *Mycobacterium smegmatis* CCM 2067, *Rhodotorula rubra* and *Saccharomyces cerevisae* ATCC 9763 were used. According to our results, the extracts prepared from *Bufo viridis* skin secretion have high antimicrobial activity against the tested microorganisms.

Key words. - *Bufo viridis*, Amphibia, antimicrobial activity, skin secretion.

Introduction

Amphibians have skin glands producing mucous and poison. Amphibians have been studied and have attracted special attention from a toxicological point of view. Various substances with antimicrobial activity have been isolated from skin secretions of amphibian species (Dapson, 1970; Croce et al., 1973; Dapson et al., 1973; Preusser et al., 1975; Cevikbas, 1978). Several toxins in amphibian poisons have been used as experimental tools and contributed to significant progress in physiology. Some toxins (Batrachotoxins) specifically block the inactivation of the voltage regulated Na^+ channels in nerve and muscle cells, which causes a massive inflow of Na^+. The cells become irreversibly depolarized, which, among other things, produces heart arrhythmia and respiratory failure and finally cardiac insufficiency. In humans, some amphibian toxins (Bufotenin) produce symptoms similar to those of LSD (Lutz, 1971; Edstrom, 1992). In previous studies, some skin secretions showed remarkable cytotoxic activity against eukaryotic cells (Kolbe et al., 1993; Sanna et al. 1993). The aim of the this study is to test the antimicrobial activity of *Bufo viridis* skin secretions against Gram-positive, Gram-negative bacteria and yeast cultures for future possible use in providing pharmacological tools for the study of new drugs and aid in benefitting human health.

Materials and Methods

Specimens of *Bufo viridis* were collected from different regions in Bursa, Turkey in March 1998. Collected frogs were brought to the laboratory and kept in an aquarium. Before experimentation, the frogs were washed first with tap water and then with distilled water. They were placed for 3-5 minutes in a glass jar containing a piece of cotton soaked with ether to stimulate skin secretions. The secretion accumulated on the skin was obtained by scraping the body of the animals with a spatula. The foamy secretion thus obtained was placed in a tube, left in an 80°C water bath for 30 min and centrifuged at 5,500 rev/min for 30 min. After centrifugation, the precipitate was used in the experiments. Before using in the experiments, the precipitate was diluted with distilled water 0.1 M HCl, 0.1 M NH_4OH, and 1 M phosphate buffers (pH: 4 and pH: 7).

In this study, *Escherichia coli* ATTC 10536, *Listeria monocytogenes* ATCC 19117, *Klebsiella pneumoniae* UC57, *Salmonella typhi* ATCC 19430, *Staphylococcus aureus* ATCC 6538P, *Mycobacterium smegmatis* CCM 2067 bacteria cultures and *Rhodotorula rubra* and *Saccharomyces cerevisae* ATCC 9763 yeast cultures were used.

In vitro antimicrobial activity studies were carried out by the Agar-Disc Diffusion Method. Mueller Hinton Agar (Oxoid) was preferred as the most suitable medium for antimicrobial activity studies. Each extract was implemented into a sterile disc in varying concentrations starting from 20 µl. Each disc was 6 mm in diameter.

Bacteria and yeast cultures were suspended in 4-5 ml Brain Heart Infusion Broth (Oxoid) and Malt Extract Broth (Difco). Bacteria were incubated in 37°C for 2-5 hours. Yeast cultures were incubated in 30°C for 5-7 hours. A visible turbidity was obtained at the end of this time. The turbidity of bacterial suspension was adjusted

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Table 1. Antimicrobial activity of various extracts of *Bufo viridis* skin secretions on microorganisms.

Microorganisms / solvents	0.1 N HCl	0.1 N NH_4OH	Phosphate Buffer pH: 4	Phosphate Buffer pH: 7	Distilled water
Escherichia coli ATCC 10356	++	+++	(+)	(+)	++
Listeria monocytogenes ATCC 19117	+++	+++	++	++	++
Staphylococcus aureus ATCC 6538P	+++	++	++	++	+++
Klebsiella pneumoniae UC57	+++	++	+++	++	+++
Salmonella thyphi ATCC 19430	+++	++	+++	++	++
Mycobacterium smegmatis CCM 2067	+++	+++	++	++	+++
Rhodotorula rubra	+++	+++	+++	+++	++
Saccharomyces cerevisiae ATCC 9730	+++	+++	+++	+++	+++

(+) : Inhibition zone less than 1 mm surrounding the 6 mm paper disk.
+ : Inhibition less than
++ : Inhibition comparable to
+++: Inhibition more than 10 µg penicillin or sulconazole / disk; Inhibition zones of references : 12-16 mm diameter.

according to Macfarland Standard Tube [0,5] with physiologic serum and inoculation performed. Prepared bacterial suspension was mixed with a sterile applicator and excess fluid of applicator was removed by rotating the applicator to one side of the tube. We streaked the entire Mueller Hinton Agar surface in three different directions by rotating the plate 60° angles after each streaking. Yeast cultures were inoculated into Muller Hinton Agar (10^2 cfu/ml). All petri dishes after inoculation were allowed to dry for 15-20 min at room temperature (bacteria at 35°C and yeast at 30°C). Inhibition zone diameters were measured after 24-48 hours (Collins et al. 1987, NCCLS 1993). In addition, continued only solvent was used as negative control disc and antibiotic penicillin and sulcanozole discs were used as references. Experiments were repeated three times and results were expressed as average values.

Results and Discussion

Antimicrobial activity effects of five different extracts, which were prepared by using distilled water, 0.1 N HCl, 0.1 N NH_4OH, 1 M phosphate buffers (pH: 4 and pH: 7), were obtained from the skin secretions of *Bufo viridis* against bacteria and yeast cultures, results are given in Table 1.

According to our findings, all the extracts of skin secretion against the yeast cultures exhibit higher antimicrobial activity than that of a compared antibiotic. The 0.1 M HCl extract shows more effect than that of the other extracts against bacteria. 1 M phosphate buffer (pH: 4 and 7) extracts exhibited minor effects against *Escherichia coli*. However, phosphate buffer (pH: 4 and 7) extracts exhibited strong effects against the other bacteria. It can be said that the active substance obtained from *Bufo viridis* skin secretion dissolves easily in the 0.1 M HCl and has high antimicrobial activity as a consequence. It has been reported that sensitivity of the microorganisms to the chemotherapeutic agents changes from strain to strain (Cetin et al., 1989). Our results are in agreement with the other authors' results.

Inhibition zone diameters around the control disc were measured as 0-1 mm. In this study, antimicrobial effects of the prepared extracts on the tested microorganisms were determined by using different solvents.

Croce et al. (1973) investigated antimicrobial activity of skin secretions from *Bombina variegata pachypus*. They homogenized skin secretion with phosphate buffers (pH: 4 and 7) 1 M HCl, 1 M NH_4OH and distilled water. These homogenates show high antimicrobial activity against *Staphylococcus aureus* but they do not show any antimicrobial effect against *Aspergillus niger*, *Trichophyton mentagrophytes* ATCC 8757 and *Candida albicans*.

Cevikbas (1978) examined antibacterial activity in the skin secretions of *Rana ridibunda*. The author reported that skin secretion of *Rana ridibunda* shows antibacterial activity at different levels. However, in our

present study, skin secretions of *Bufo viridis* against the yeast cultures shows more antimicrobial activity than that of the bacterial cultures. Our findings parallel those reported in the above studies. In Amphibia, antimicrobial activity of skin secretions differ at both the generic and specific levels.

Although the antimicrobial activity of skin secretions from *Bufo viridis*, *Bufo vulgaris*, *Salamandra maculosa* and *Salamandra atra* were determined (Pavan, 1962; Pavan and Nascimbene, 1948), antimicrobial activity of skin secretion from *Bufo marinus*, *Triturus,* and *Xenopus* were not observed (Preusser et al., 1975; Kolbe et al., 1993; Ozeti and Yilmaz, 1994). Antiyeast activity observed in our study was not observed in Croce's et al. study (1973). Our results show that skin secretion components from *Bufo viridis* may be different from *Bombina variegata pachymus*.

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Analysis of the Stomach Contents of the Lycian Salamander *Mertensiella luschani* (Steindachner, 1891) (Urodela: Salamandridae), Collected from Southwest Turkey

SERDAR DÜŞEN, MEHMET ÖZ, AND M. RIZVAN TUNÇ

Akdeniz University, Faculty of Arts and Sciences, Department of Biology, 07058, Antalya, Turkey

Abstract. - In this paper, the stomach contents of 116 specimens (39 males, 47 females, and 30 juveniles) from the Southwest Turkey *Mertensiella luschani* populations are analyzed. A total of 342 prey items were identified and their frequency of occurence and percent of diet were tabulated. The majority of the diet consisted of Insecta (50.58%), and within Insecta, Coleoptera (65.32%) was the major order represented. In addition to insects, *M. luschani* feeds on Gastropoda (19.59%), Arachnida (16.08%), Myriapoda (8.57%), Clitelliata (3.50%) and Crustacea (1.75%).

Key words. - *Mertensiella luschani*, stomach contents, prey, southwest Turkey.

Introduction

Nine subspecies of the Lycian Salamander, *Mertensiella luschani,* are distibuted along the coast of Southwestern Turkey and on some islands (e.g., Kastellorizon, Meis, Kekova, and Karpathos) (Baran and Atatür, 1997; Başoğlu et al., 1994; Veith et al., 2001). These are *M. l. luschani* Steindachner, 1891, *M. l. helverseni* Pieper, 1963, *M. l. atifi* Başoğlu, 1967, *M. l. fazilae* Başoğlu and Atatür, 1974, *M. l. finikensis* Başoğlu and Atatür, 1975, *M. l. antalyana* Başoğlu and Baran, 1976, *M. l. basoglui* Baran and Atatür, 1980, *M. l. billae* Franzen and Klewen, 1987, and *M. l. flavimembris* Mutz and Steinfartz, 1995. *Mertensiella luschani* is not dependent on water, it inhabits humid soils and crevices under the *Pinus brutia* forests, Mediterranean maquis, and open rocky areas. Its vertical distribution ranges between 15-1300 m.

Various studies have been done on *M. luschani* in terms of its taxonomy (Franzen et all, 2001), ecology (Klewen, 1991; Steinfartz and Mutz, 1998), and reproductive biology (Özeti, 1973; Özeti, 1980). The aim of

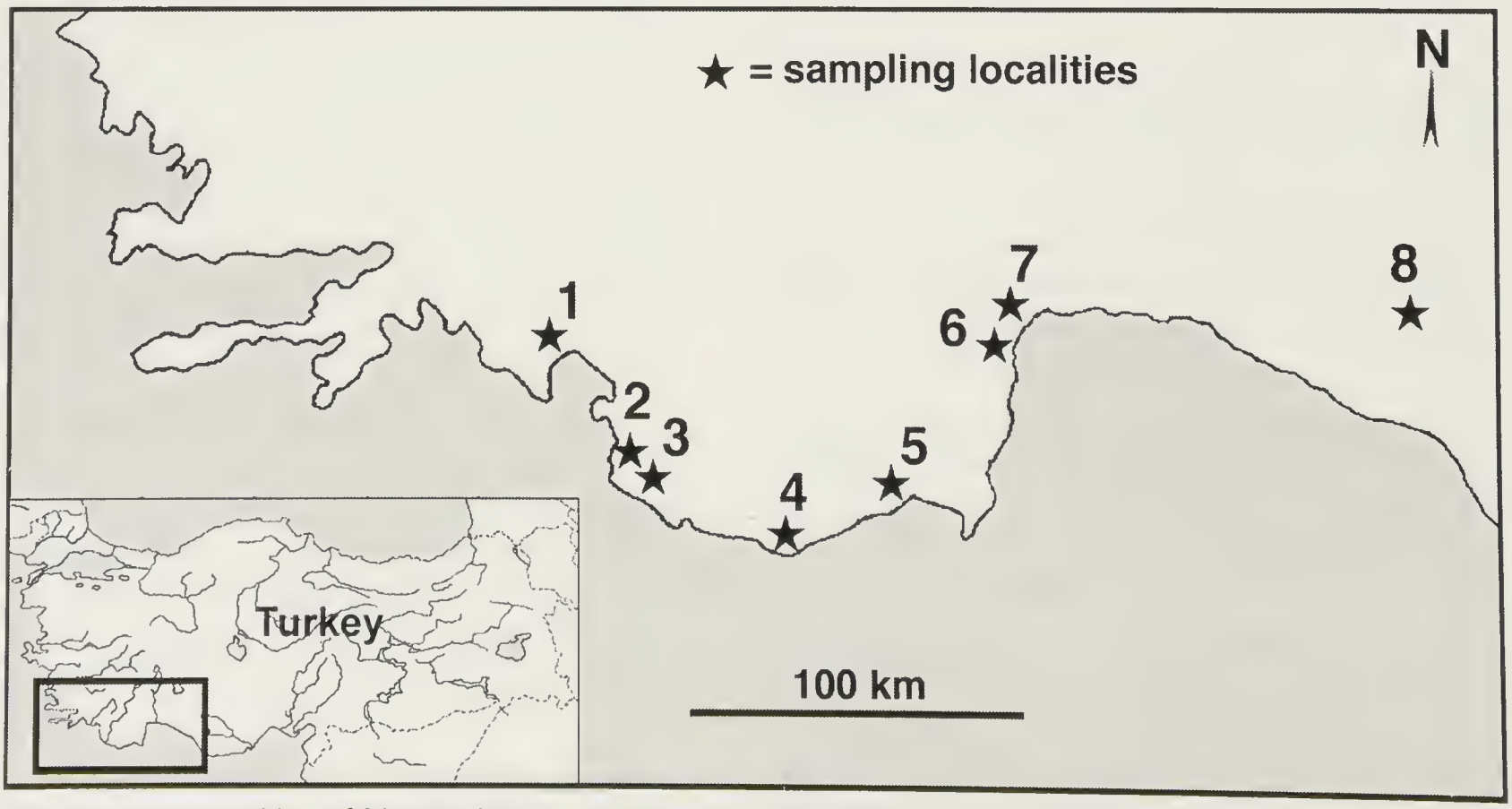

Figure 1. Collecting localities of *Mertensiella luschani* in Southwest Turkey. 1-Kocagöl, 2-Dodurga, 3- Letoon, 4-Nadarlar, 5-Finike, 6-Büyükçalt1cak, 7-Hurma, 8-Fersin

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Table 1. Composition of the stomach contents of *Mertensiella luschani* (39 males, 47 females, 30 juveniles) collected from the Southwest Turkey. **N**: The numbers of every prey found in all stomachs. **n**: The number of stomachs every prey type was found in.

Taxon	N	(%)	n	(%)
GASTROPODA				
Pulmonata	67	19.59	36	31.03
CLITELLIATA				
Neogliochaeta (=Prospora)				
Lumbricidae	12	3.50	9	7.75
CRUSTACEAE				
Isopoda	6	1.75	6	5.17
MYRIAPODA				
Diplopoda	1	0.29	1	0.86
Julidae	17	4.97	14	12.07
Chilopoda	8	2.34	6	5.17
Geophilidae	3	0.88	3	2.58
ARACHNIDA				
Aranae	37	10.82	27	23.27
Pseudoscorpionida (=Chelonethi)	18	5.26	15	12.93
INSECTA				
Collembola (=Podura)	4	1.17	3	2.58
Dermaptera				
Forficulidae	8	2.34	8	6.89
Isoptera	1	0.29	1	0.86
Heteroptera	4	1.17	5	4.31
Lygaidae	3	0.88	1	0.86
Homoptera	1	0.29	1	0.86
Coleoptera	113	33.04	51	43.96
Hymenoptera				
Formicidae	31	9.06	19	16.37
Diptera	3	0.88	3	2.58
Lepidoptera	5	1.46	5	4.31

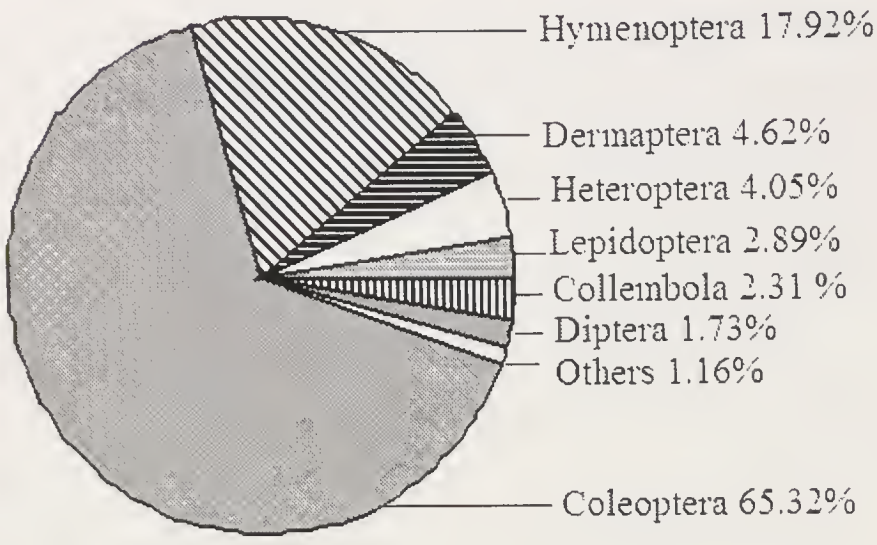

Figure 2. Distribution of the insect groups in numerical percentages.

the present preliminary investigation on seven *M. luschani* subspecies (except *M. l. flavimembris and M. l. helverseni*) from eight localities in Southwest Turkey is an analysis of stomach contents.

Materials and Methods

Specimens for this study were collected from the eight localities in Southwest Turkey during the known activity period of *M. luschani* (December-February, 1999). A total 116 (39 males, 47 females, and 30 juveniles) *M. luschani* specimens were collected by hand under stones. Collection sites are shown in Figure 1.

Once collected, the salamanders were taken to the laboratory to undergo stomach-flushing. A thin pipe wash bottle is inserted in salamander's esophagus and stomach. Gentle pressure on the wash bottle forces distilled water in to the stomach and forces the food out throught mouth (modified from Gittins, 1987). The prey items obtained from each specimen were labeled and stored in 10 cc. bottles containing 70% ethanol. Dried pieces from both undigested and partially digested prey were placed on microscope slides and held in place with cellophane tape (Düşen and Öz, 2001). These pieces consisted of whole body, wings, thorax with abdomen, head, and mouth parts. Through this approach, identification to the lowest taxonomic categories was attempted, samples were examined using a stereomicroscope with 10-25x magnification. Prey items were identified and grouped utilizing methods described elsewhere (Demirsoy, 1998a,b; Grzimek, 1979a,b; Lodos, 1986; Riehm, 1984)

Results

We did not observe any significant differences in the stomach contents of seven subspecies males, females and juveniles; they were thus evaluated together. Of the 116 specimens (39 males, 47 females, and 30 juveniles), only two females had empty stomachs. Small unrecognizable insect remains (parts of heads and larvae, antennae, wings, etc.) of the stomach contents are not included to the numerical analysis. Other non-food materials such as small pebbles, sand grains, plant particles, and pieces of feather, possibly ingested during prey capture were not included either.

A total of 342 prey items were counted from the investigated stomach contents (Fig. 2); Insecta 173 (50.58%), Gastropoda 67 (19.59%), Arachnida 55 (16.08%), Myriapoda 29 (8.57%), Clitelliata 12 (3.50%) and Crustacea 6 (1.75%). Table 1 presents the stomach contents with respect to prey groups (their taxonomic grouping, number of prey items, and percentages of preyers).

Insects were identified to the ordinal level. The total number of prey and their percentages are as follow: coleopters 113 (65.32%), hymenopterans 31 (17.92%), dermapterans 8 (4.62%), heteropterans 7 (4.05%), lepidopterans 5 (2.89%), dipterans (1.73%), collembolan 4 (2.31%), homopterans 1 (0.57%), and isopterans 1 (0.57%) (Fig. 2). The same insect orders can be ranked from the viewpoint of the number of prey eaten; their percentages are as follows: coleopterans 51 (43.96%),

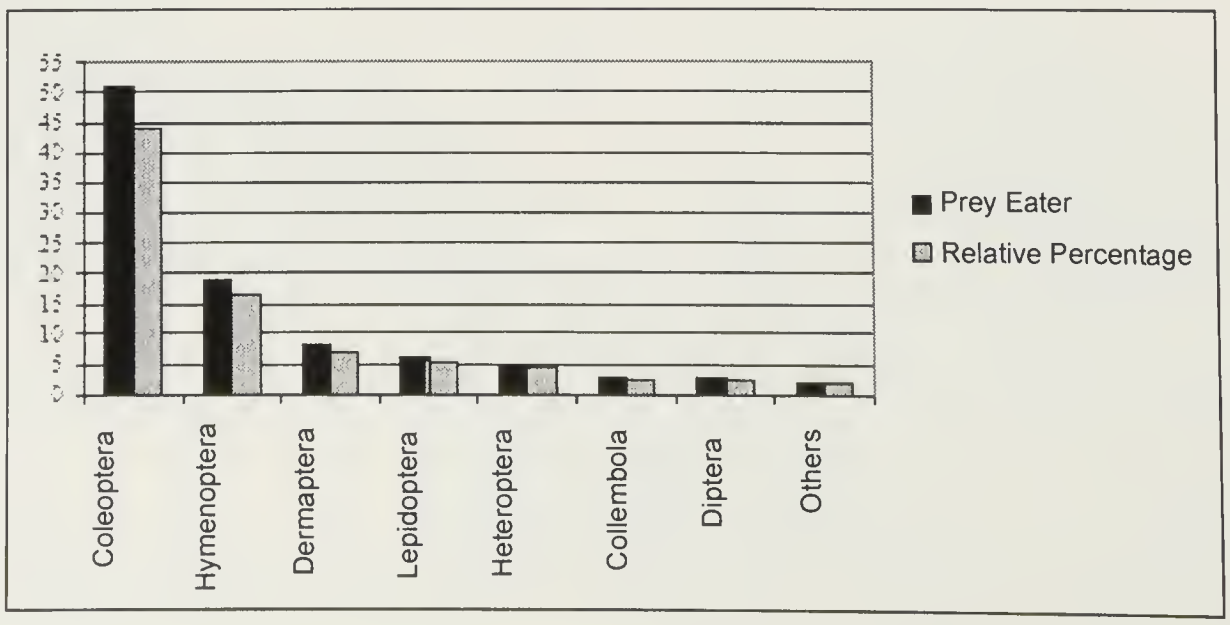

Figure 3. Distribution of the insect groups regarding prey eaters.

hymenopterans 19 (16.37%), dermapterans 8 (6.89%), heteropterans 6 (5.17%), lepidopterans 5 (4.31%), collembolans 3 (2.58%), dipterans 3 (2.58%), homopterans 1 (0.86%), and isopterans 1 (%0.86) (Fig. 3).

When the prey groups are evaluated by their absolute values and relative percentages within the food, coleopterans 51 (43.96%), have the priority. Other consumed invertebrates as follows: Pulmonata 36 (31.03%), Aranae 27 (23.27%), Pseudoscorpionida 15 (12.93%), Diplopoda 15 (12.93), Clitelliata 9 (7.75%), Chilopoda 9 (7.75%), and Isopoda 6 (5.17%).

Discussion

This study was conducted to learn more about the feeding preferences of *M. luschani* collected from southwest Turkey. The results showed that *M. luschani* feeds heavily on coleopters and gastropods.

The chance of a food item being taken depends on the abundance and ease of capture of the different food categories. Coleopters, although fairly fast moving are abundant in the foraging area. Gastropods and arachnids although easier to catch are slightly less abundant.

The results suggest that *M. luschani* is an opportunist predator on diverse forms. This situation is related to the type of habitat they live in and abundance of prey species in the vicinity.

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First Description of Egg Sacs and Early Larval Development in Hynobiid Salamanders (Urodela, Hynobiidae, *Batrachuperus*) from North-Eastern Iran

MEHREGAN EBRAHIMI[1], HAGI GHOLI KAMI[2], MATTHIAS STÖCK[3]

[1]*Department of Biology, Faculty of Sciences, University of Shiraz, P.O.Box:71454-1460, Shiraz, Iran; E-mail: emehrgan@yahoo.com*

[2]*Department of Biology, Faculty of Sciences, University of Agricultural Sciences and Natural Resources, P.O.Box:49165-386, Gorgan, Iran; E-mail: hgkami2000@yahoo.com*

[3]*Museum of Vertebrate Zoology, University of California, Berkeley, Department of Integrative Biology, 3101 Valley Life Sciences Building #3160,Berkeley, CA 94720-3160, USA; E-mail: matthias@berkeley.edu*

Abstract. - Here we present the first life history data from a natural habitat on the clutch and from the laboratory on the early embryonic development of an Iranian hynobiid salamander (the Eastern nominal taxon, *Batrachuperus gorganensis*). We compare these observations with those of other hynobiid species. The egg sac of *B. gorganensis* varied from 80 to 182 mm (mean 132.5), and in width from 16 to 22.5 mm (mean 18.9). Single sacs, the largest known for the genus, contained 31-52 eggs (mean 37.4) in four rows per cross section. Egg sac data are more similar to those of *Ranodon sibiricus* (and *B. mustersi*) than to Eastern *Batrachuperus* (*longdongensis*, *tibetanus*, *pinchonii*, *karlschmidti*, *yenyuanensis*), which have strings of single eggs. As is typical of all *Batrachuperus*, eggs of *B. gorganensis* are non-pigmented. Embryonic *B. gorganensis* larvae may exhibit rudimentary balancers, possibly like those of *Ranodon sibiricus*, but further investigation is necessary. Detailed morphometric measurements of the larvae of *B. gorganensis* and color photographs of some developmental stages are presented.

Key words. - Hynobiidae, *Batrachuperus*, *Batrachuperus gorganensis*, *Batrachuperus persicus*, *Batrachuperus mustersi*, *Ranodon sibiricus*, Iran, egg sacs, embryonic development, larvae, balancer, taxonomy, morphometrics.

Introduction

The southwestern-most representatives of the salamander family Hynobiidae occur within the narrow, East-West oriented Hyrcanian Corridor (= Hyrcania) of Northern Iran. The corridor is a "unique relict biogeographic area," which is "well defined as the south-western and southern shores of the Caspian Sea ..." and is "one of the most clearly defined and delineated provinces in the Irano-Turanian region" (Fet, 1994). The Persian mountain salamander, *Batrachuperus persicus* Eiselt and Steiner, 1970, was based on larvae collected from the western part of Hyrcania (NW-Iran, mountains near Asalem, Gilan province; Eiselt and Steiner, 1970). Subsequently, specimens that metamorphosed in captivity were described and several additional localities were reported (see Schmidtler and Schmidtler, 1971; Steiner, 1973).

The second nominal taxon, *Batrachuperus gorganensis* (Clergue-Gazeau and Thorn, 1979), was described from a single adult male type discovered in a cave from the eastern edge of the Hyrcanian Corridor (Clergue-Gazeau and Farcy, 1978). Baloutch and Kami (1995), Kami and Vakilpoure (1996) as well as Kami (1999, 2004) published additional data on the biology and distribution of Iranian hynobiid salamanders, all assigned to *B. persicus*. Stöck (1999) provided a flow-cytometric DNA measurement (34.77 pg, but based on GC-biased DAPI-staining, see also Litvinchuk et al., 2004) and a Giemsa-stained karyotype (2n = 62) of topotypic *B. gorganensis* (i.e. the eastern taxon). Stöck also described external larval changes during the development from 40 mm until metamorphosis (100 mm), and reviewed previous papers (see also map with geographic coordinates of all previously published localities – Stöck, 1999: Fig. 1). After examination of topotypic subadults and larvae of both taxa as well as morphometric comparisons with *B. mustersi, B. pinchonii,* and *Ranodon sibiricus*, Stöck considered a clinal variation of characters between the western (*B. persicus*) and the eastern nominal taxon (*B. gorganensis*) possible (see also Thorn and Raffaëlli, 2001: 122). However, molecular and cytogenetic data as well as a continuous examination of the morphological variation throughout the Hyrcanian corridor are lacking.

Both nominal Iranian taxa (cf. Anderson, 1985; Brame, 1985: 567; Duellman and Trueb, 1986: 497; Thorn and Raffaëlli, 2001) are considered two out of currently nine species of the genus *Batrachuperus* (Frost, 2002). Risch (1984) regarded *gorganensis* to belong to a separate genus (*Paradactylodon*; see Reilly, 1987). While the molecular phylogeny of eastern

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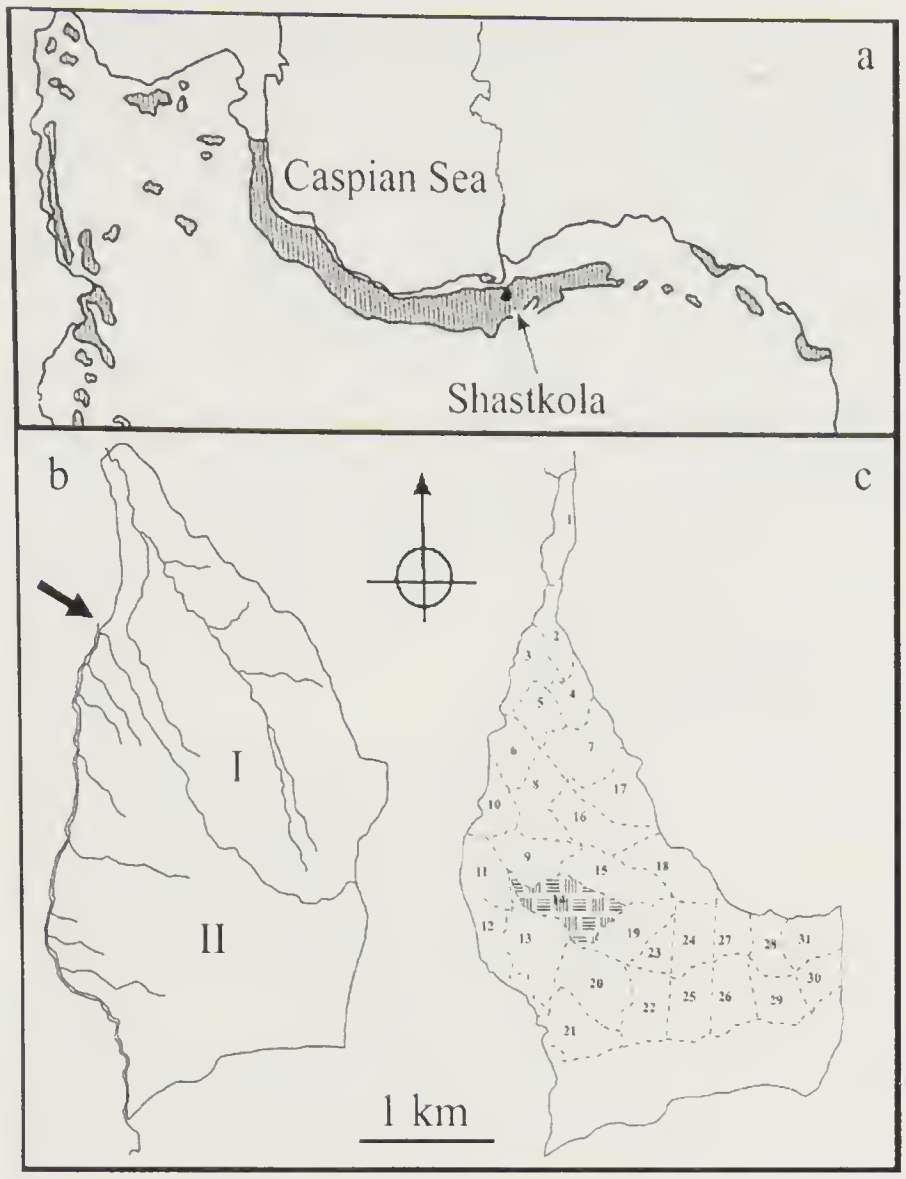

Figure 1. Locality: **a**. Sketch map of northern Iran with its forested regions and the study area, the educational forest of Shastkola; **b**. Shastkola forest with districts I and II and streams. The left arrow marks the Shastkola river; **c**. District II of Shastkola forest shown in (b) with its 31 land parcels, the spring of Manzoulak is situated in parcel 14.

Batrachuperus has been examined (Fu et al., 2001), molecular comparisons of their relationships with Western *Batrachuperus* and *Ranodon* as well as between the latter taxa are not yet available. However, unpublished results (Macey et al. in prep., with phylogram presented in Larson et al., 2003: 44, Fig. 2.4) provide evidence that Iranian *Batrachuperus* may be more closely related to *Ranodon* (Kazakhstan, China) and *B. mustersi* (Afghanistan) than to the Eastern *Batrachuperus* species (Tibet, China). *Ranodon sibiricus* has five toes on the hind limbs while *B. mustersi,*and *B. persicus*/*B. gorganensis* have only four. However, the intraspecific variation found by Reilly (1983) in *B. mustersi*, which sometimes has five instead of four toes, demonstrates how ambiguous this character can be.

In general, there is still a lack of biological data on the Iranian taxa, e.g., their egg sacs and early larvae have never been examined. Only remains of egg cases of *B. persicus* were found by Steiner (1973) in late July in the Central Elburz range and the reports on larvae start from a minimum size of 22.7 mm (Central Iran; Steiner, 1973) and "about 30 mm" (NW-Iran, Schmidtler and Schmidtler, 1970). Here we present the first data on the clutch of the Eastern Hyrcanian hynobiid taxon (*B. gorganensis*) from a natural habitat. We add some data on its development in the laboratory and compare these observations with the features known from other hynobiid species.

Results and Discussion

Spawning site. - All clutches (Table 1) were found in Cheshme-ye (= spring of) Manzoulak (36°42′ N, 54°21′ E), which flows into an artificial pond (3.20 x 2.15 x 1.25 m). Its bottom is covered with a thick layer (*ca.* 15 cm) of tree leaves. Some crabs (*Potamon* sp.) and larvae of Odonata, Trichoptera, Coleoptera, Ephemeroptera were observed. Manzoulak spring is one of the important water resources of the Shastkola educational forest (3716 ha), which is situated 13 km South-West of Gorgan city between 36° 41′- 36° 45′ N and 54° 20′ - 54° 24′ E, on the northern slopes of the Elburz mountains (Fig. 1). These mountains reach elevations ranging from 240 m, above the Caspian Sea in the North to 2168 m (Gholle-ye-leila Kouh). Shastkola forest is divided into two organizational units, districts I (1698.6 ha) and II (2017.4 ha). The spring is situated in II [Fig. 1c, land parcel 14 (75 ha), 650 m to 830 m]. Outcrops consist mainly of a sequence of sandstones and schist in the lower part and Triassic sand stones in the upper parts. Shastkola forest has a Caspian climate, and the nearest climate station is Gorgan (155 m a.s.l.). However, local climate at the breeding site differs considerably from that at the foothills and we currently have no detailed climatic data on the site. Water temperature during collection was below 10°C. The forest tree and shrub species include *Fagus orientalis, Carpinus betulus, Parrotia persica, Ruscus hyrcana, and Ilex aquifolia* (for further information: Azadfar, 1994; Azadfar and Darghahi, 2002), which adds to the accumulating evidence that the Iranian hynobiid taxa inhabit humid regions mainly overgrown with the plant assemblage *Fagetum hyrcanum* in lower elevations in the West of their range: *Parrotio-Carpinetum*; in eastern parts of the Elburz N-slope: *Carpinetum orientalis*, *Quercus macranthera*; see also ref. in Stöck, 1999).

Description of clutches, eggs and larvae. - About 70 clutches and four adult salamanders were discovered when leaves were removed from the pond by G. Yolmeh on January, 28, 2002, but only two of the clutches and one adult specimen (total length: 211 mm) were sent to the Museum of Zoology of Gorgan University (ZMGU). In the following year on February, 8, 2003, one complete and two incomplete clutches were collected in the same pond by M. Ebrahimi and G. Soltanpour. We presume that spawning, at least at this site, happened between the second half of January and the first days of February.

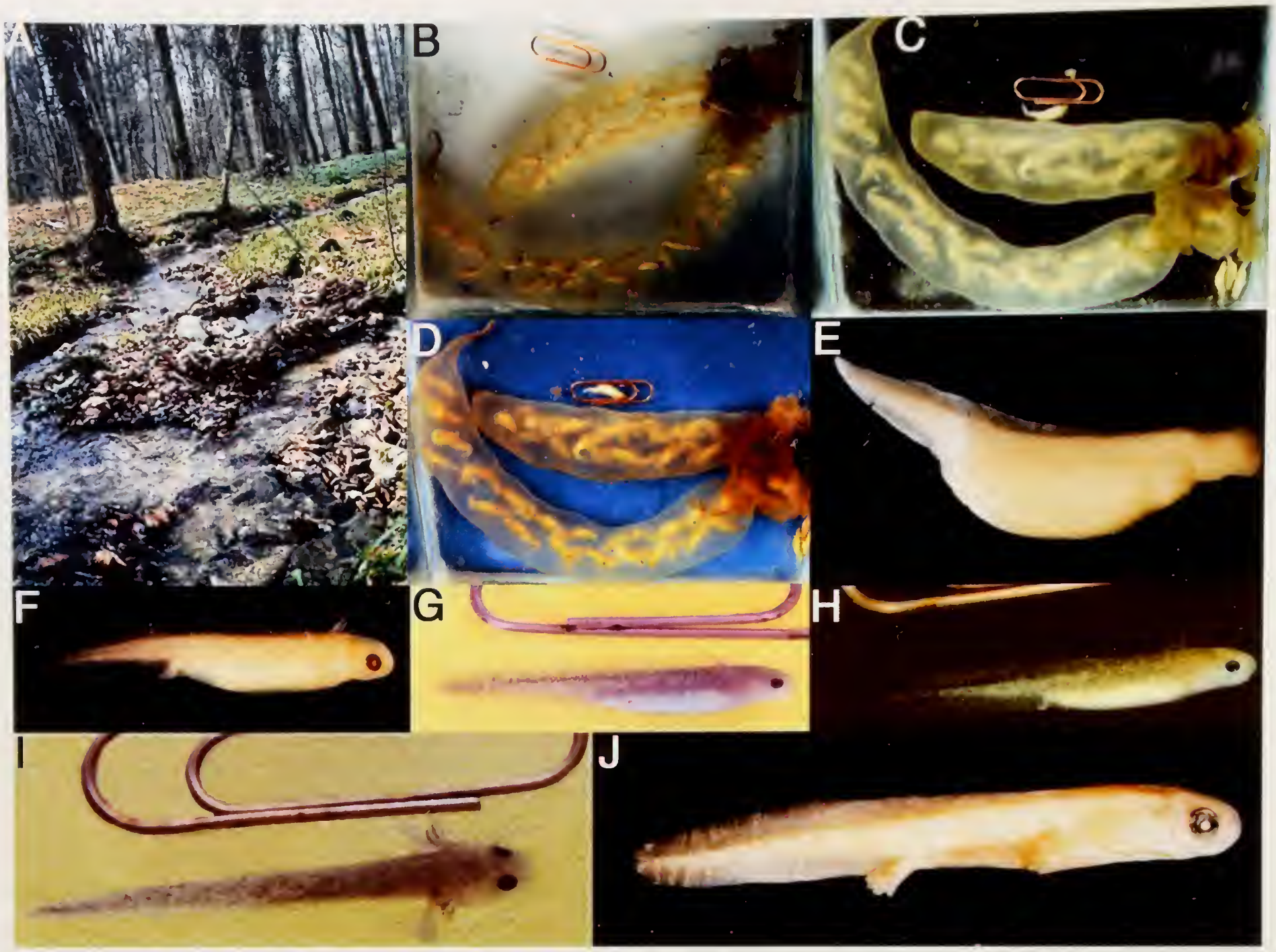

Figure 2 (A-J). **A**. Natural habitat of *Batrachuperus gorganensis*. Stream near Manzoulak spring, photograph taken: March, 10, 2003. **B**. Clutch, preserved, collection date: March, 10, 2003, photograph taken: April, 6, 2003. **C**. Clutch, collection date: March, 10, 2003, photograph taken: April, 4, 2003. **D**. The same clutch as in C, collection date: March, 10, 2003, photograph taken: April, 4, 2003. **E**. Fixed embryo, 7 days before hatching, photograph taken: October, 9, 2003. **F**. Fixed larva, 4 days after hatching, photograph taken: October, 9, 2003. **G**. Living larva, 18 days after hatching, photograph taken: April, 6, 2003. **H**. Living larva, 18 days after hatching, photograph taken: April, 6, 2003. **I**. Living larva, 24 days after hatching, photograph taken: April, 6, 2003. **J**. Fixed larva, 34 days after hatching, photograph taken: October, 9, 2003.

However, in general, the breeding season in both Iranian nominal taxa might last as long as in some other Hynobiids (e.g. in *Ranodon sibiricus* from the end of April until the beginning of August - Kuzmin, 1995: 111; from May to beginning of August in *B. karlschmidti* - Liu, 1950: 91).

During collection, some egg sacs broke. Originally, the clutches were attached by their stalks to a stone at the corner of the pond; no egg sacs were observed on its walls. As is usual in *Batrachuperus*, each clutch consisted of two asymmetrical, colorless, cylindrical gelatinous sacs that were connected by gelatinous filaments forming an attaching stalk and had free filaments at their nonanchored conical ends. As in *Ranodon sibiricus* (see Kuzmin, 2001: 40), egg sac data varied between and within clutches (see Fig. 2 B-D; Table 1). Each cylindrical gelatinous sac contained four rows of eggs per cross section and each egg was surrounded by a spherical gelatinous envelope. As is known from *Ranodon sibiricus* (see Kuzmin and Thiesmeier, 2001: 42 and ref. therein), these four egg rows produce a tetrahedral shape immediately after clutch deposition. However, as the result of an ingress of water, sacs later strongly increase in size. We believe that all discovered clutches had already finished this first swelling, which usually gradually continues throughout the embryonic development leading to a considerable enlargement of the sacs until hatching. Tables 2 and 3 show comparisons of egg sac length and width of eight hynobiid species. Data on length and width should be evaluated with some reservations, because the number of specimens examined or time after clutch deposition is imperfectly known. However, egg sacs of *B. gorganensis* probably are larger than those of any of the close relatives of the taxon (with the possible exception of *B. longdongensis*) and appear to contain among the highest number of eggs per

Table 1. Overview of described clutches of *Batrachuperus gorganensis*.

Date of collection	Number of egg sacs	Length of gelatinous egg sac (mm)		Maximum width of gelatinous egg sacs	Total number of eggs per sac		Date of hatching	Live hatched larvae	
		Left	Right		Left	Right		N	%
January, 28, 2002	1	95	102	16.5	9+9+10+11=39	9+9+8+9=35	Fixed	-	-
	2	80	81	15.8	34	35	Fixed	-	-
February, 2, 2003	1	150.5	172.6	-	31	38	March, 19 to 24, 2003	51	74
	2	182.5	destroyed	20.8	32	40	All died	-	-
	3	181	181.8	22.4	38	52	March, 19 to 24, 2003	64	71.1
	4	-	-	-	Small part of an egg sac, 18		Fixed	-	-
	5	100.9	-	-	Small part of an egg sac, 30		March, 21 to 24, 2003	28	93.3

sac (Table 4). In addition, *R. sibiricus* and *B. gorganensis* share the common feature of four rows of eggs per cross section in an egg sac, while all Eastern taxa (*B. longdongensis, B. tibetanus, B. pinchonii, B. karlschmidti, B. yenyuanensis*) seem to have only a single row of eggs in an egg case (judging from photographs and Zhao and Hu, 1988: 32). This feature remains obscure in *B. mustersi*, since neither Reilly's (1983) description nor Nawabi's (1965) photograph resolve the question satisfactorily, but more than a single row appears to be present. Egg number may be a taxonomic character but might not affect fecundity since some species seem to deposit more than one clutch per breeding period (Liu, 1950; Reilly, 1983).

The diameter of the initially yellowish (as in all *Batrachuperus* and *R. sibiricus*) eggs varied from 4.10 to 5.00 mm (mean 4.56; n = 10) when the clutch was found. The early eggs had a white animal pole whereas the vegetal pole was pigmented gray. Unfortunately, early eggs were not photographed. The separation of eggs in a row was less than the diameter of an egg. Egg number varied from 7 to 11 per row (2 egg sacs examined) and from 31 to 52 in each sac (see Table 1). The eggs have substantial amounts of yolk, as also is typical of stream-breeding *R. sibiricus* (Kuzmin and Thiesmeier, 2001).

Three complete clutches and one incomplete clutch were kept in a refrigerator at 5-7°C (for conditions see Stöck, 1999). The first larvae to hatch were found on March, 19, 2003, and the latest specimens to hatch were observed on March, 25, 2003 (i.e. 40 to 46 days after discovery, respectively). Some larvae at different developmental stages were fixed in 4% formalin and 70% alcohol and measurements were taken from all specimens (summarized in Table 5). We report some larval developmental traits and link them by inserting the approximate stage (see inserted number in [...]) of normal development for *Ranodon sibiricus* drawn by Kuzmin and Thiesmeier (2001: 46, after the description of Lebedkina, 1964).

Hatching larvae [stage 1] exhibited limb buds (Fig. 2F). Although no balancers were observed in hatched larvae (Fig. 2F), we believe that a rudimentary structure observed in an embryo fixed 7 days before hatching (Fig. 2E) could be a balancer. These enigmatic, ephemeral larval organs, found in three of the ten families of salamanders (Crawford and Wake, 1998), are present in many species of Hynobiidae (Crawford and Wake, 1998: 115). In the presumed close relative of the Iranian hynobiids, *B. mustersi* (see introduction), distinct balancers are well documented (Nawabi, 1965, see also Reilly, 1983). Although such a well developed

Table 2. Egg sac length of eight* hynobiid species, comparison of available data on *Batrachuperus mustersi* from Nawabi (1965), Reilly (1983), and Sparreboom (1979); on *R. sibiricus* (from Brushko and Narbaeva 1988, cited from Kuzmin and Thiesmeier 2001); *B. gorganensis* (our data); *B. longdongensis*, *B. tibetanus*, *B. yenyuanensis* from Fei and Ye (2001), *B. pinchonii* and *B. karlschmidti* from Liu (1950) and Fei and Ye (2001); in *R. sibiricus* numbers in parentheses show rare values in late stages of embryonic development (* some authors synonymized *B. karlschmidti* with *B. tibetanus*, but see Fu et al. 2001 and Frost 2002).

	B. gorganensis	*R. sibiricus*	*B. mustersi*	*B. longdongensis*	*B. pinchonii*	*B. karlschmidti*	*B. tibetanus*	*B. yenyuanensis*
Mean	**132.48**	?	**96.62**	-	-	**96.6**	-	-
Max	182	100 (390)	150	200	96	96	140	125
Min	80	65 (100)	60	-	65	75	102	70
N	10	10	13	-	-	5	-	-

Table 3. Egg sac width of eight hynobiid species, comparison of available data; same sources as in table 2; the only available value for *R. sibiricus* is from an egg sac of 72-75 mm length.

	B. gorganensis	*R. sibiricus*	*B. mustersi*	*B. longdongensis*	*B. pinchonii*	*B. karlschmidti*	*B. tibetanus*	*B. yenyuanensis*
Mean	**18.88**	**(23)**	**21.02**	-	-	**16.6**	-	-
Max	22.4	-	27.0	15	12	19	10	8
Min	15.8	-	13.2	-	19	14	12	15
N	10	-	13	-	-	5	-	-

organ is absent in *Ranodon sibiricus* (cf. Crawford and Wake, 1998: 115), the presence of rudimentary balancers in the species appears possible. Regel (1968: 17, see "pb" in her Fig. 7, transl. from Russian) wrote on *R. sibiricus* larvae in developmental stage 3 (15-17 mm): "On the lateral surface of the distal end of the palatinoquadratum cartilage an excrescence develops, which is a rudimentary proc. balancer (Rusconi's hook)". Although balancers are not cartilaginous structures, Kuzmin and Thiesmeier (2001: 43) quote this as an indication of rudimentary balancers in *Ranodon.* Based on these observations, we believe that at least rudimentary balancers will be found in *B. gorganensis* (and *B. persicus*?), and we recommend further comparative investigation with histological methods. Secondary loss of well developed balancers may be an adaptation of the "limnophilous mountain brook type" of larvae in *B. gorganensis / B. persicus* (discussed in Stöck, 1999: 237). According to available data, balancers may be absent in all species of *Batrachuperus* from China and Tibet (Table 4).

In larvae eight days after hatching (d.a.h.) [stage 2-3], the head had differentiated and forelimbs had a shovel-like form, but only hind limb buds were visible. The yolk sac regressed and was very small in larvae 14 d.a.h. (April, 2nd, 2003). In larvae 16-18 d.a.h. [stage 6-7] (Fig. 2G-H), the yolk sac had disappeared, dark spots became visible at the back, and the tail fin developed, although development of the digits was incomplete (April, 4, 2003). In larvae 24 d.a.h. [stage 8-9] (Fig. 2I), digits were well developed in forelimbs, but the toes of hind limbs were still incomplete (April, 12, 2003). In larvae 34 d.a.h. [stage 12] (Fig. 2J) the forelimbs were completely developed, digits were clearly distinguishable, and tips of all digits and toes exhibited brown horny claws. The ventral surface had a milky color, the upper part of the tail and the tail fin showed dark spots, and the eyes appeared completely developed. Through time, the dark spots became more abundant at the tip of tail, and the mouth. Darkly pigmented dots appeared on part of the head and trunk, the flanks, the upper parts of the tail, and the upper tail fin. At this stage, larvae were fed with nauplius larvae of *Artemia.* In larvae 46 d.a.h., the belly remained spotless, but the flanks, dorsal body parts and upper parts of the tail showed dark spots. Larvae 62 d.a.h. exhibited brownish spots on the body and dark spots became rarer (larger larvae had golden dots on the gills and on parts of the body). The anterior part of the upper tail fin extended to the occiput.

In addition to the clutches described above, more than 20 large larvae with a total length of almost 10 cm were collected in the leaves of the breeding pond, but only one adult specimen was found. The pond was searched completely, but no larvae smaller than about 10 cm were found. Therefore, we conclude that all these large larvae apparently stemmed from the preceding year. The growth rate data of the larvae hatched from the clutches in our laboratory fit well with the later developmental stages reported by various previous authors from natural habitats (summarized in Stöck, 1999: Tab. 3).

Table 4. Number of eggs per sac, number of egg rows per cross section and presence of a balancer of eight hynobiid species, comparison of available data; same sources as in table 2, except for *B. longdongensis* in which the character was inferred from the ovary of voucher MVZ 208610.

	B. gorganensis	*R. sibiricus*	*B. mustersi*	*B. longdongensis*	*B. pinchonii*	*B. karlschmidti*	*B. tibetanus*	*B. yenyuanensis*
Mean	**37.40**	**23.00**	**22.23**	-	-	-	-	-
Max	52	44	31	-	23	12	25	13
Min	31	7	13	-	5	7	16	6
N	10	150	13	-	-	5	-	-
Rows of eggs per cross section	4	4	>2	1(-2)?	1	1	1?	1?
Balancer	rudimentary	rudimentary?	well developed	No?	No?	No	No?	No?

d.a.h.		total length	head length	body length1	body length2	tail length	head width	eye diame-ter	min. dist. eye to snout	foreleg length	hind leg length	distance between feet	max hight dorsal fine	dis-tance snout to ant. point dorsal fin	number of rec-ognized costal grooves	mass (g)
1	MEAN	19.28	2.40	11.05	11.63	7.49	2.54	0.73	0.89	0.65			1.04	4.01		0.05
1	MIN	19.05	2.25	10.80	11.40	7.06	2.00	0.67	0.77	0.50			1.00	3.50		0.05
1	MAX	19.61	2.50	11.40	11.80	7.80	2.95	0.80	0.97	0.80			1.05	5.00		0.05
1	SD	0.28	0.11	0.25	0.17	0.37	0.40	0.06	0.09	0.15			0.03	0.67		0.00
	N = 4 (1)															
4	MEAN	19.30	2.67	11.00	11.73	7.37	2.45	0.77	0.90	0.65			1.12	3.50		0.05
4	MIN	18.50	2.40	10.50	11.20	7.00	2.30	0.70	0.90	0.55			1.10	3.00		0.04
4	MAX	19.79	2.90	11.40	12.10	7.60	2.65	0.85	0.90	0.80			1.15	4.00		0.06
4	SD	0.70	0.25	0.46	0.47	0.32	0.18	0.08	0.00	0.13			0.03	0.50		0.01
	N = 3 (1)															
8	MEAN	21.76	2.79	12.11	12.73	8.86	3.19	0.96	1.06	1.34			1.33	5.09		0.07
8	MIN	21.27	2.25	11.80	12.20	8.40	2.75	0.90	0.90	1.00			1.10	4.75		0.06
8	MAX	22.20	3.60	12.50	13.00	9.40	3.50	1.02	1.22	1.70			1.50	5.50		0.08
8	SD	0.30	0.53	0.27	0.29	0.37	0.26	0.04	0.11	0.23			0.12	0.23		0.01
	N = 8 (1)															
14	MEAN	24.61	3.28	13.68	14.44	10.15	3.61	1.03	1.22	2.14	0.70	7.97	1.45	5.90		0.10
14	MIN	23.13	2.65	12.76	13.50	9.50	2.90	0.95	1.00	1.50	0.55	7.45	1.35	4.00	11	0.09
14	MAX	25.53	3.70	14.00	14.90	10.70	4.10	1.10	1.45	2.60	0.90	8.25	1.60	8.00	14	0.12
14	SD	0.92	0.39	0.41	0.53	0.44	0.47	0.06	0.14	0.35	0.14	0.26	0.09	1.29		0.01
	N = 7(1)															
16	MEAN	27.06	4.03	14.65	15.54	11.47	3.86	1.19	1.36	2.72	1.39	8.37	1.49	6.56		0.12
16	MIN	26.45	3.25	14.10	15.10	10.36	3.50	0.95	1.00	2.00	1.00	8.15	1.40	5.05	12	0.11
16	MAX	27.93	4.40	15.54	16.65	12.00	4.00	1.30	1.55	3.10	1.55	8.60	1.55	8.15	14	0.15
16	SD	0.43	0.35	0.41	0.48	0.53	0.17	0.10	0.16	0.32	0.19	0.16	0.05	0.86		0.01
	N = 9															
19	MEAN	24.87	3.28	13.83	14.56	10.09	2.83	1.08	1.08	1.86	1.41	8.56	1.22	5.29		0.06
19	MIN	20.90	2.35	11.80	12.50	8.00	2.00	0.75	0.75	0.75	0.25	7.25	0.95	3.00	13	0.04
19	MAX	36.90	5.40	19.79	20.53	16.28	5.30	1.80	1.70	5.20	4.00	9.70	2.15	8.00	14	0.21
19	SD	4.28	0.80	2.04	2.10	2.32	0.88	0.29	0.28	1.21	1.22	0.88	0.30	1.69		0.04
	N =15 (3)															
24	MEAN	26.67	3.70	14.75	15.63	10.77	3.11	1.09	1.18	1.78	0.60	8.93	1.30	4.94		0.08
24	MIN	22.94	3.00	13.30	14.10	8.90	2.65	0.90	0.85	1.25	0.50	8.00	1.10	3.50		0.07
24	MAX	30.15	4.80	16.40	17.20	13.00	3.75	1.30	1.65	2.50	0.75	9.70	1.50	7.75		0.11
24	SD	2.58	0.76	1.26	1.22	1.49	0.43	0.17	0.27	0.44	0.13	0.86	0.14	1.53		0.02
	N = 6 (2)															
34	MEAN	30.46	4.68	16.33	17.12	13.10	4.15	1.43	1.67	3.15	1.91	8.95	1.58	6.92		0.13
34	MIN	29.04	4.20	15.20	16.10	12.10	3.80	1.25	1.50	2.30	0.80	8.40	1.50	6.00	12	0.11
34	MAX	32.74	4.90	16.90	17.60	14.20	4.50	1.65	1.80	3.80	2.85	9.50	1.70	8.50	12	0.16
34	SD	1.71	0.25	0.60	0.53	0.79	0.26	0.16	0.13	0.62	1.00	0.42	0.08	0.97		0.02
	N = 6 (2)															
46	MEAN	31.69	4.42	16.58	17.56	13.95	4.18	1.40	1.59	3.53	2.19	8.92	1.45	7.83		0.10
46	MIN	28.12	4.00	16.00	16.80	12.30	3.30	1.15	1.20	2.10	1.00	8.50	1.25	7.00		0.07
46	MAX	33.80	4.75	17.57	18.68	15.30	5.00	1.60	1.90	4.55	3.70	9.50	1.65	9.00		0.13
46	SD	2.03	0.25	0.56	0.68	1.12	0.72	0.17	0.27	1.03	1.24	0.48	0.15	0.67		0.02
	N = 6 (3)															
54	MEAN	31.78	4.71	17.24	18.13	14.08	4.23	1.35	1.53	3.32	1.72	8.66	1.61	7.23		0.13
54	MIN	25.90	3.35	14.90	15.70	10.50	3.00	1.05	1.25	1.95	0.50	7.60	1.40	5.00	12	0.08
54	MAX	36.20	5.50	19.24	20.35	16.66	5.50	1.65	1.90	4.75	4.10	9.40	2.05	9.50	13	0.22
54	SD	3.69	0.73	1.65	1.78	2.26	0.94	0.22	0.26	1.03	1.14	0.51	0.22	1.57		0.05
	N = 8 (3)															
62	MEAN	34.65	5.50	18.52	19.43	15.60	4.90	1.38	1.53	4.12	2.40	9.40	1.92	7.90		0.24
62	MIN	31.82	4.60	16.70	17.60	13.50	4.30	1.15	1.25	3.35	1.60	8.70	1.55	7.50	12	0.16
62	MAX	37.20	6.00	20.35	21.27	16.65	5.40	1.50	1.75	4.60	3.20	10.00	2.25	8.60	12	0.32
	SD	2.70	0.78	1.83	1.84	1.82	0.56	0.20	0.26	0.67	0.80	0.66	0.35	0.61		0.08

Table 5 (previous page). Morphometric data on early larvae of *Batrachuperus gorganensis*.
d.a.h. = days after hatching; SD = standard deviation; Min = minimum; Max = maximum;
N = number of larvae measured (the value in parentheses shows from how many clutches the measured larvae originated)

According to these studies, larvae from the first season may reach a total length of 30 to 62 mm (*persicus*, between June and August) and 41 to 50 mm (*gorganensis*, mid of June), respectively, and must overwinter before they form "large larvae", which can enter metamorphosis in the following year.

Conclusions and Future Research

Our initial studies support the relationship of the three taxa *Ranodon sibiricus*, *Batrachuperus mustersi* and the Iranian hynobiid(s), i.e. *B. persicus* and *B. gorganensis*. These taxa have apparently more features in common than with the *Batrachuperus* taxa East of Tibet. In addition to the essential need for molecular data, it would be valuable and interesting to study egg deposition in the natural habitats in more detail and to collect data throughout the range of the Iranian hynobiid salamanders, especially from the central and western portions. During proof reading, one of us (HGK) provided information that MMTT 452, 453, and 454 are eggs of *B. persicus*, found near the road from Asalem to Khalkhal, collected May, 20, 1975, by M. Thireau, R. Khazaie and R. G. Tuck.

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Histochemical Characterization of the Lingual Salivary Glands of the House Gecko, *Ptyodactylus hasselquistii* (Squamata: Gekkonidae)

Bashir M. Jarrar and Noory T. Taib

Zoology Department, College of Science, King Saud University, P.O.Box 2455, Riyadh 11451 Saudi Arabia.

Abstract. - Histochemical investigations of the lingual salivary glands of the house gecko, *Ptyodactylus hasselquistii* have been conducted. The glands are comprised of mucous and mucoserous cells. Mucous cells secrete or elaborate neutral mucosubstances, neuraminidase sensitive carboxylated mucins, hyaluronidase resistant sulfomucins, but are devoid of proteins. The mucoserous cells secrete and elaborate neutral mucosubstances and glycoproteins but are devoid of sialomucins and sulfomucins. The results are discussed in the context of the feeding habits and phylogeny of reptiles.

Key words. - Histochemistry, lingual, salivary glands, house gecko, *Ptyodactylus hasselquistii*, Gekkonidae.

Introduction

Histochemical studies on the lingual salivary glands of vertebrates have mainly been concerned with mammals, whereas little attention has been paid to the lingual salivary glands of non-mammalian vertebrates. Most studies on the lingual salivary glands of reptiles have focused with morphological and histological aspects while few histochemical studies have been carried on these glands (Raynaud, 1961; Gabe and Saint-Girons, 1969; Lopes et al., 1982; Taib and Jarrar, 1985a; 1985b; 1985c; 1986; Taib, 1986, Asgah et al., 1990). Nevertheles, the literature on the lingual secretions of lizards is rather scanty and their consitituents have yet to be determined.

The present study is a detailed histochemical characterization of the lingual salivary glands of the house gecko, *Ptyodactylus hasselquistii*.

Materials and Methods

Twenty adults of each male and female house gecko *Ptyodactylus hasselquistii* were trapped from different houses in Riyadh city, Saudi Arabia. They were killed by etherization and the whole tongue was removed from each animal and quickly immersed for 24 hrs in one of the following fixatives: neutral buffered formalin, Bouin's fluid and Gendre's fluid. They were then thoroughly washed in running water, processed for serial sectioning at 4-5 µm thickness and the sections were stained with haematoxylin-eosin or with Mallory trichrome for histological examination, whereas the secretary cells of the glands were characterized by the criterion of Gabe and Saint-Girons (1969). Other sections were used for the following histochemical reactions:

Neutral mucosubstances. - Periodic acid-Schiff (PAS) technique (Gurr, 1962), PAS after diastase digestion (McManus and Mowry, 1964), PAS after alpha-amylase digestion (Luna, 1968), PAS after acetylation blockade (McManus and Cason, 1950), PAS after acetylation-saponification (Oxello et al.,1958), PAS after phenylhydrazine treatment (Spicer et al., 1967) and PAS after treatment with chloroform and methanol.

Acid mucosubstances. - Alcian blue (AB) at pH 2.5, 1.0, and 0.4 (Mowry, 1956; Luna, 1968).

Distinction between acidic and neurtal mucosubstances. - AB (pH 2.5)-PAS (Mowry and Winkler, 1956) and AB (pH 1.0)-PAS (Spicer et al., 1967).

Distinction between sulfomucins and sialomucins. - Aldehyde fuchsion (AF) and AF-AB, pH 2.5 (Spicer and Meyer, 1960); weak (25°C, 16 hr), mild (37°C, 4hr) and strong (60°C h hr) methylation-saponification- AB (PH 2.5) (Spicer, et al., 1967); toluidine blue (TB) buffered at pH 1.7 and 3.4 (Landsmeer, 1951), critical electrolyte concentration (CEC) technique for extinction of alcianophilia at pH 5.6 in the presence of gradual concentation of Mg^{2+} (Scott and Dorling, 1965).

Enzyme digestion tests. - Diastase-PAS technique (McManus and Mowry, 1964); neuraminidase (Sialidase, Vibrio chlolerae, type V)-AB (pH 2.5) (Spicer and Warren, 1960); hyaluronidase (testicular)-AB (pH 2.5) (Spicer et al., 1967). Ribonuclease digestion (Love and Rabotli 1963); neuraminidase-TB (pH 3.7), hyaluronidase-TB (pH 2.0) were employed. In each case control sections were incubated for the same length of time at the same temperature in buffer solutions without the enzyme.

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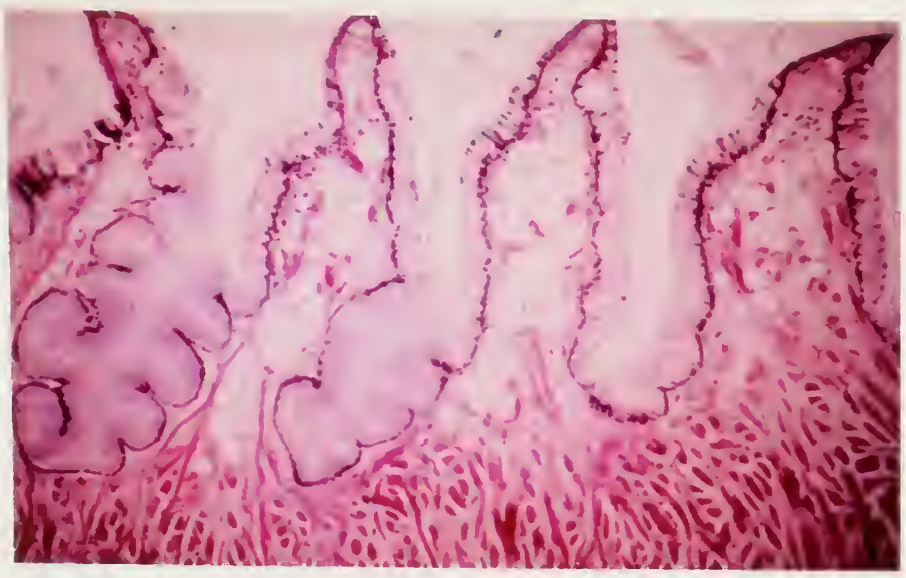

Figure 1. Lingual glands of *P. hasselquistii* after staining with haematoxylin-eosin. Note that the mucous cells of the lingual glands are located in the papillar space of the papillae. x950.

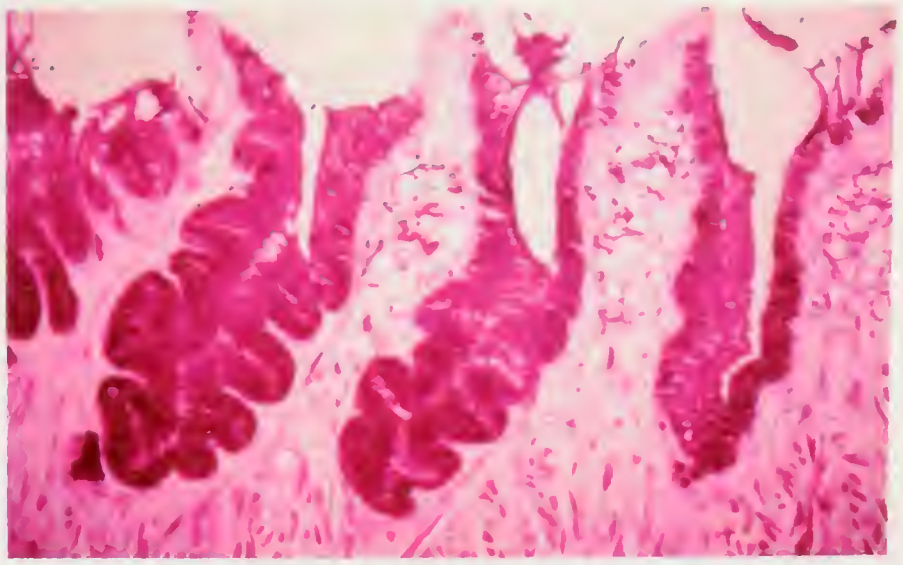

Figure 2. Lingual glands of *P. hasselquistii* after staining with PAS. The reactivity of the glands confirms the presence of the neutral mucosubstances. x950.

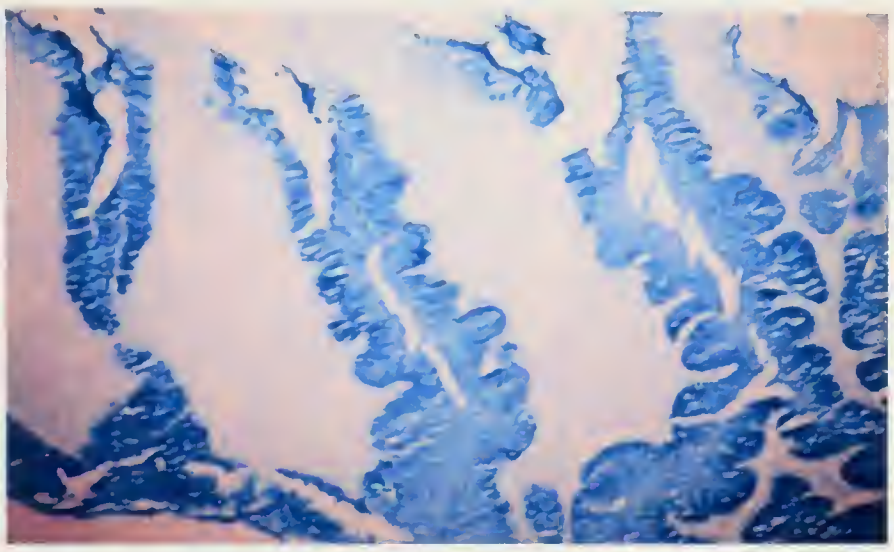

Figure 3. Lingual glands of *P. hasselquistii* after staining with AB (2.5), confirming the presence of sialomucins and sulfomucins. x950.

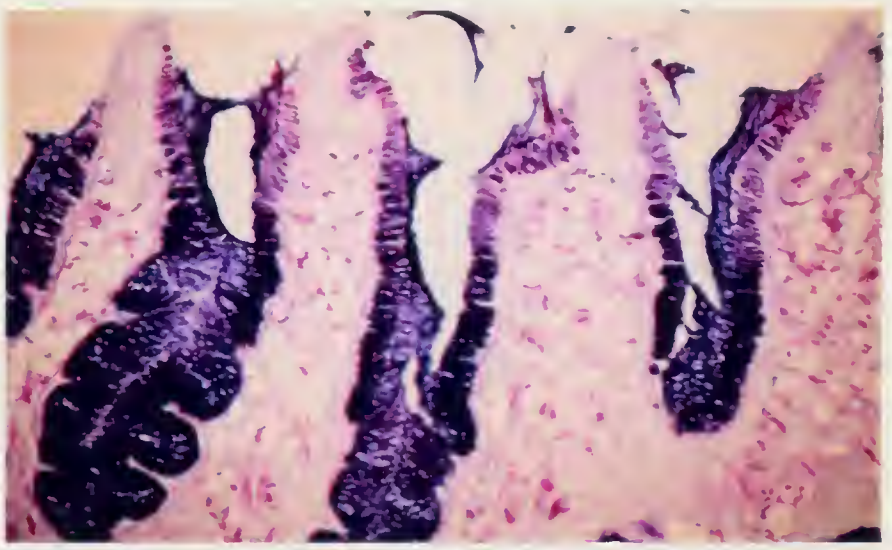

Figure 4. Lingual glands of *P. hasselquistii* after staining with AB (1.0)-PAS. The bluish purple color indicates the presence of neutral and sulfated mucosubstances simultaneously. x950.

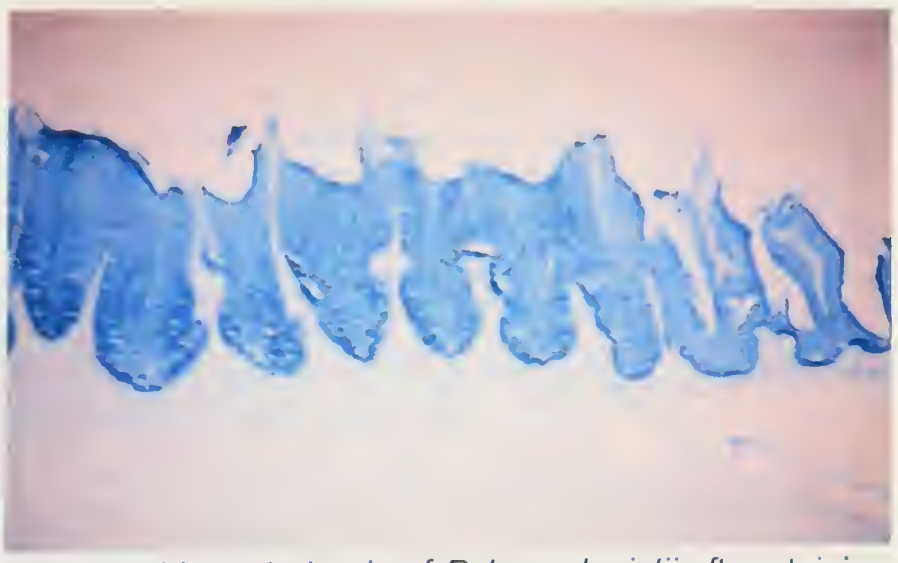

Figure 5. Lingual glands of *P. hasselquistii* after staining with CEC at 0.3M Mg^{++}., confirming that the mucosubstances produced by the glands contain carboxyl and sulfated groups. x950.

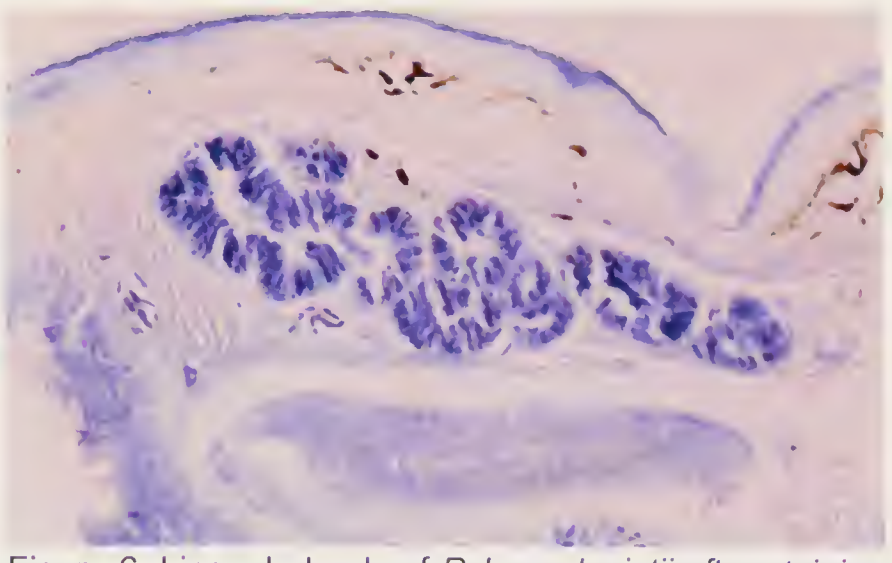

Figure 6. Lingual glands of *P. hasselquistii* after staining with MBPB, indicating the protein contents of the glands secretion. x700.

Proteins. - Mercuric bromophenol blue method (Mazia et al., 1953); ninhydrin-Schiff (Yasuma and Itchikawa, 1953), mercuric-bromophenol blue (MBPB) and PAS after trypsin digestion (Pearse, 1972).

Photographs. - Photographs were taken with a 35mm Zeiss Ikon camera on Kodacolor NR 100 film.

Results

The lingual salivary glands of the house gecko, *Ptyodactylus hasselquistii* occupy the papillar invagination of the posterior two-thirds of the dorsal surface together with the lateral sides of the tongue. The anterior part of the tongue is devoid of any glandular structure and covered by keratinized squamous epithelium. These glands are made of mucous cells located in the inner papillar space of the filiform papillae (Fig. 1) together with simple tubular structures made of mucoserous cells seen at the most posterior part of the dorsum. The mucous cells have an alveolar cytoplasm and flattened, basally located nuclei with clear apical ends resting on a delicate basement membrane.

As summarized in Table 1, the mucous cells of the lingual glands of *P. hasselquistii* exhibited strong PAS reactivity (Fig. 2) which was neither labile to alpha-amylase nor to saliva digestion but completely lost by phenylhydrazane treatment. However, this reactivity was completely blocked by acetylation and was partly restored by deacetylation-PAS sequential techniques. They showed marked alcianophilia at both pH 2.5 (Fig. 3) and 1.0 but to lesser extent at pH 0.4. They also reacted with both PAS and AB and stained bluish purple with AB (2.5)- PAS and AB (1.0) PAS (Fig. 4). These glands also reacted with AF as well as with AF-AB (2.5) and AF-AB (1.0). The alcianophilia of the glands was partly lost at pH 2.5 with acid hydrolysis and weak methylation and there after restored by saponificiation techniques. They demonstrated alcianophilia with the CEC techniques at 0.1M, 0.2M, and to some extent at 0.3M Mg^{2+} (Fig. 5) and showed metachromasia at pH 3.4 and 1.7 but reacted negatively to all protein detection tests.

The mucoserous cells of the glands showed PAS reaction, exhibited no alcianophilia at pH 2.5 and 1.0 and were orthochromatic at pH 3.4 and 1.7 but reacted positively to all protein detection tests (Fig. 6). No sexual dimorphism was observed in the lingual secretion of the species under study.

Discussion

The lingual salivary glands present great diversity in morphology amongst the various groups of reptiles. These glands are entirely absent from Varanidae, Amphisbaenia, Ophidia and some species of Chelonia such as *Chelonia mydas* (Kochva, 1978). On the other hand, these glands are simple consisting of three different types of goblet cells in most species of Testudinidae (Nalvade and Varute, 1976; Taib and Jarrar, 1984). Some lizard possess mainly goblet cells together with simple tubular glandular structures in their tongues (Nalvade and Varute, 1976; Shevliuk, 1976; Taib and Jarrar 1985 b; 1985c and 1986), while others have more developed lingual salivary glands as seen in some Agamidae, Iguanidae, Gekkonidae, Anguidae and Chamaleonidae (Gabe and Saint-Girons, 1969; Kochva, 1978; Asgah et al., 1990). On the bases of the results of the present study and in view of the criterion of Gab and Saint-Girons (1969), the lingual salivary glands of *Ptyodactylus hasselquistii* are made of unicellular mucous goblet cells lining the dorsal epithelium of the tongue with mucoserous simple tubular glandular apparatus at the base of the tongue. The structure of the lingual salivary glands of *P. hasselquistii* is different from those of *Tupinambis teguixin*, *Agama blandfordi*, *Uromastyx microlepis*, *Acanthodactylus schmidti* and *Scincus mitranus*, which have only mucous cells in their lingual glands (Lopes et al, 1974; Taib and Jarrar, 1985b; 1985c; 1986; Taib, 1986). According to Gabe and Saint-Girons (1969), the lingual glands are mucous in Gekkonidae, mucoserous on Sphenodontidae, Anguidae and Pygopodidae, but seromucous in Chamaleonidae and serous in some speices of Iguanidae and Agamidae. The grading from non-glandular tongues through unicellular with or without simple tubular glandular structure to only simple tubular and to then tubulo-alveolar ones may reflect developmental stages towards the definitive lingual glands of higher vertebrates (Shevliuk, 1976; Kochva, 1978).

A tentative interpretation of the types of mucosubstances in the lingual glands of *P. hasselquistii* can be made from the results of the different histochemical reactions used in the present investigation and from the classification of mucosubstances proposed by Mowry and Winkler, 1956; Spicer and Meyer, 1960; Scott and Dorlling, 1965; Pearse, 1972). Neutral mucosubstances are PAS positive, diastase resistant, as well as unstainable by cationic dyes. Acetylation produces derivatives of primary and secondary amines which prevent 1, 2 glycol groups, from reacting with PAS indicating the presence of neutral mucosubstances or sialic acid, separately or simultaneously. Alcian blue is generally considered as being specific for identifying acid mucosubstances where alcianophilia at pH 2.5 and 1.0 is specific for sialomucins and sulformucins respectively (Mowry and Winkler, 1956). In the combined aldehyde fuchsin-alcian blue sequential techniques, sulfomucins stain purple blue and sialomucins blue (Spicer and Meyer, 1960).

Table 1. The histochemical reactions in the lingual salivary glands of *Ptyodactylus hasselquistii*.

Histochemical reaction	Results	
	MC	MSC
PAS	++,P	++,P
Diastase digestion -PAS	Nb	Nb
Acetylation-deacetylation-PAS	++,p	++,p
Phenylhdrazine-PAS	Cb	Cb
AB (pH 0.4)	+B	-
AB (pH 1.0)	+B	-
AB (pH 2,5)	++, B	-
AB (pH 1.0) -PAS	+,Bp	-
AB (pH 2.5)-PAS	++,Bp	-
AF	+,P	-
AF- (AB pH 1.0)	+,Bp	-
AF- (AB pH 2.5)	++,Bp	-
Acid hydrolysis- AB (pH 2.5).	Pb	-
W. methylation - AB (2.5)	Pb	-
W. methylation-saponification - AB (pH 2.5)	++,Bp	-
M. methylation-AB (pH 2.5)	Cb	-
M. methylation-saponification -AB (pH 2.5)	+,B	-
S. methylation-AB (pH 2.5)	Cb	-
S. methylation-saponification- AB (pH 2.5)	+,B	-
TB (pH 1.7)	+	-
TB (pH 3.4)	+	-
CEC (AB, 0.1 M)	+	-
CEC (AB, 0.2 M)	+	-
CEC (AB, 0.3 M)	±	-
CEC (AB, 0.5 M)	-	-
Neuraminidase-AB (pH 2.5)	+B,pb	-
Hyaluronidase-AB (pH 2.5)	++B,Nb	-
Ninhydrin-Schiff	-	+
Hg- bromophenol blue	-	+
Chloramine T-Schiff	-	+
Trypsin digestion-PAS	Nb	-
(Chloroform + methanol)-PAS	Nb	-

Reactions: - negative; ± weak; +, moderately positive; ++, intensely positive; Cb, complete blockade; M, mild; Pb, partial blockade; Nb, no blockade; S, strong; TB, toluidine blue; W, weak.
Colors: B, blue; Bp, bluish purple; P, pink.
Glands: MC, mucous cells; MSC, mucoserous cells.

Sialomucins can be identified by alcianophilia at pH 2.5 which is partially lost following acid hydrolysis and completely removed after neuraminidase digestion, but neuroaminidase did not affect the staining of sulfated mucosubstances. A loss of alcianophilia after hyaluronidase digestion is due to the removal of hyaluronic acid and chondroitin sulfates. Methylation blocks subsequential stainig of simple mucosubstances by esterification of carboxyl groups and complex sulfated mucosubstances desulphation. Subsequent treatment with potassium hydroxide (saponification) after methylation will restore the staining of carboxyl groups (Drury et al., 1967). The mucosubstances that are stained at 0.1M $MgCl_2$ in the CEC reaction, but not at 0.2M $MgCl_2$ are believed to contain carboxyl group and no sulfate groups. Sulfated mucosubstances, on the other hand, stain strongly and selectively at 0.2M Mg^{2+} but lose their alcianophilia at different levels with increasing $MgCl_2$ concentration (Spicer and Lillie, 1960). The lingual glands of the species under study resisted trypsin digestion and the action of (chloroform-methanol) which excludes the possibility of lipids and proteins. Accordingly, the lingual salivary glands of of the house gecko, *Ptyodactylus hasselquistii* contain neutral mucosubstances, sialadase labile carboxylated mucosubstances and hyaluronidase resistant sulfomucins and glycoproteins.

The lingual secretions of *P. hasselquistii* are different from those of some lizards such as *Tupinambis teguixin* and *Agama blandfordii* which contain neutral

mucosbstances and sialomucins but no sulfomucius (Lopes et al., 1974; Taib and Jarrar, 1985c). They also differ from the secretions of the lingual glands of *Uromastyx microlepis*, *Acanthodactylus schmiditi*, *Scincus mitranus* and *Stenodactylus slevini* which contain neutral mucosubstances, sialomucins and sulformucins but no glycoprotein (Taib and Jarrar, 1985b, 1986; Taib, 1986; Asgah et al., 1990). Neutral mucosubstances have been demonstrated in the secretions of all studied reptiles that possess salivary glands while phylogenetically, the absence of sulfomucins in the lingual glands would favour the concept that sialomucins secretive cells are more primitive than sulfated mucosubstances secretive ones. In addition, the heterogenous histochemical recactivity of the lingual glands might have appeared in the evolutionary lines of reptiles to meet the different changes in the feeding habits of various species. Neutral mucins were present in the lingual glands of almost all studied reptile species while sialomucins together with neutral mucosubastances were identified in the lingual glands of all insectivorous reptiles so far studied (Nalvade and Varute, 1972; Taib and Jarrar, 1985c, 1986; Taib, 1986). The lingual glands of all insectivorous and carnivorous reptiles studied thusfar exhibited sulfomucins. More work is needed to elucidate whether the lingual secretion diversity of reptiles imply phylogenetic relationships or different feeding habits.

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The Biology of the Persian Mountain Salamander, *Batrachuperus persicus* (Amphibia, Caudata, Hynobiidae) in Golestan Province, Iran

HAJI GHOLI KAMI

Department of Biology, Faculty of Sciences, University of Agricultural Sciences and Natural Resources, P. O. Box 49165, Gorgan, Iran.

Abstract. - The Persian Mountain Salamander, *Batrachuperus persicus*, is a hynobiid endemic to Iran and is distributed in specific localities of Hyrcanian forests in four northern provinces of Iran. The biology of this salamander was studied at four localities in Golestan Province of Iran, especially in Shirabad Cave, between 1996 and 1999. Information is presented about the cave and other localities. This salamander has four fingers and toes. The larval stages of the salamander are found at all times of year and probably don't transform during the first year. The head form of small larvae is wider posteriorly while the head form of large larvae, juveniles and adult specimens is more or less rectangular. Juveniles have more yellow spots than adults. Juvenile and adult specimens are found inside and outside of water in the cave but in other localities they can be found in burrows around springs and are not active during the day. They feed on larval and adult forms of insects and other arthropods. Adults also feed on small specimens of bats (*Myotis blythyii*) inside of the cave. Some large specimens are cannibalistic and feed on larvae and juveniles of *B. persicus* in natural habitats and in the laboratory. This species does not hibernate inside the cave and is active all times of the year. The total length of the longest specimen was 268.5 mm.

Key words. - Amphibia, Hynobiidae, *Batrachuperus persicus*, Iran.

Introduction

The Persian Mountain Salamander, *Batrachuperus persicus* Eiselt and Steiner 1970, was described based on five salamander larvae collected near Asalem in the Talesh Mountains in Gilan Province of Iran (Eiselt and Steiner, 1970) (See editorial note and Ebrahimi et al., 2004). Subsequently J. J and J. F Schmidtler collected some larvae in Weyser, southeast of Chalus, in Mazandaran Province, Iran, in 1970. These transformed in captivity and a brief description of juvenile specimens was presented (Schmidtler and Schmidtler, 1971). Primary information was presented on adult specimens in Ardabil Province of Iran (Baloutch and Kami, 1995). New distribution records were published some years ago (Kami and Vakilpoure, 1996). Adult specimens of this species were described for the first time together with their habitats in Gilan and Ardabil provinces of Iran (Kami, 1999).

The biology of this salamander has been studied in the laboratory and in natural habitats especially in Shirabad Cave of Khanbebain. Students of Gorgan University and I have visited Shirabad Cave twelve times between 1996 and 1999. Detailed information on the other localities is sparse and these localities must be studied more in the future.

Study areas. - *Batrachuperus persicus* is distributed in the four northern provinces of Iran (Fig. 1). Figure 2 shows new localities of *Batrachuperus persicus* in

Figure 1. The four provinces of Iran that encompass the distribution of *Batrachuperus persicus*. 1- Ardabil; 2- Gilan; 3- Mazandaran; 4- Golestan.

Golestan Province. Most of the research was done at locality 1 (Shirabad Cave), other localities were visited only one time. Climatic information for five cities of Golestan Province is summarized in Table 1.

Locality 1. Shirabad Cave- Shirabad Cave (36° 57' N, 55° 03' E) is situated 70 km East of Gorgan, southeast of Khanbebain and Shirabad Village at about 420 m above sea level (Fig. 3, 4). The cave and waterfalls were designated as a National Park by the Department of

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Tab 1. Summary of climatic information (15 years) in five cities of Golestan province of Iran.

station (city)	elevation (m)	Annual precipitation (mm)	Mean of Air temperature (ºC)	Mean of minimum temperature (ºC)	Mean of maximum temperature (ºC)	Mean of relative moisture (%)	Annual evaporation (mm)
Azadshahr	129	847.6	17.1	0.7	31.9	71.6	--
Ramian	200	883.1	16.2	-1.0	35.0	65.0	497.0
Minoudasht	155-180	765.3	17.3	-1	36.0	82.1	482.5
Gonbad-e-kavous	30-45	388.3	18.2	-3.5	36.5	68.6	510.0
Gorgan	160	642.7	17.7	2.8	36.4	---	---

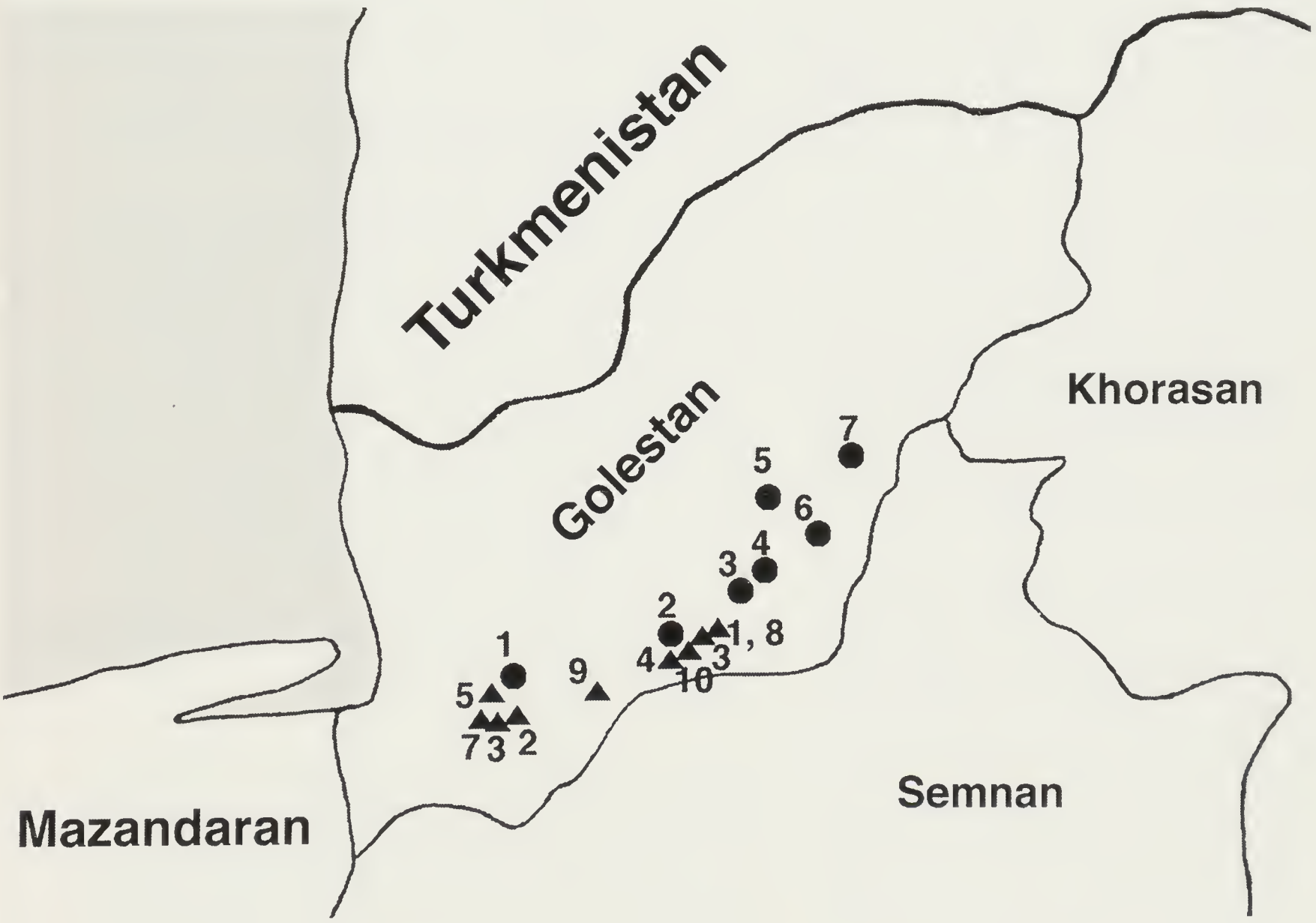

Figure 2. Localities of of *Batrachuperus persicus* in Golestan Province, Iran: 1- Shirabad Cave, 2 - Vantakhteh; 3- Near Shirabad Cave; 4- Spring of Khouklou; 5- Barankouh (36° 45' N, 54° 25' E), about 10 km south west of Gorgan, almost 1100 m elevation; 6- Spring of Khonakou, situated south southwest of Gorgan, Jahannama Protected Area, Valley of Sorkhcheshmeh, below elevations of Pir-e-zan (elevations of Pahlavan Ghaleh), 1800 m elevation; 7- elevations of Yakhkesh (36° 42' N, 54° 23' E) about 15 km south of Gorgan, 2300 m elevation; 8- Water falls of Shirabad; 9- Valley of Loushan, inside of valley, (36° 42' N, 54° 41' E) about 30 km southeast of Gorgan; 10- Region of Aram-e-Sorkhcheshmeh opposite side of Siah Marzkouh, Village of Aliabad. Circles are cities: 1- Gorgan; 2- Aliabad; 3- Ramian; 4- Azadshahr; 5- Gonbad-e-kavous; 6- Minoudasht; 7- Kalaleh.

Table 2. Dates of study, air and water temperature of four localities in Golestan province of Iran.

Locality	Dates of study	Air temperature (°C)	Water temperature (°C)	Time
Shirabad Cave	1996/11/1	---	12	
	1997/2/28	---	11	
	1997/4/11	---	10-10.5	
	1997/4/17	12.5-13	11	
	1997/7/10	19.5-21	13	1045-1100
	1997/10/2-3	---	12	
	998/4/17	---	11	
	998/5/8	18	10	1200
	1998/5/15	18	13	1430
	1998/5/19	15	12	
	1998/7/10	---	13	
	1998/9/2	17	11	
Vantakhteh	1996/11/25	2-6	6.5-7	1330-1530
Near Shirabad	1997/7/10	20-23.5	19	1000
Khouklou Spring	1999/5/26	26-27	12	1230

Environment of Gorgan and Gonbad-e-Kavous in 1998. There are seven waterfalls below the cave. The entrance of the cave is about 15 m high and is at least 3-4 m high in other parts of the cave. It is almost 240 m long and is completely dark. Water emerges from the mouth of the cave and flows to the river and waterfalls at all times of the year.

No plant species live inside the cave, but there is *Lycopodium* sp on the floor of cave from the entrance to about 10 m inside of it on large flat stones. Some plant species that were identified outside the entrance of the cave on 28 February 1997 and 17 April 1997 are: *Pteridum aquilinum, Adianthum capillus-veneris, Athyrium flix-mas, Phyllitis scolopendrium, Funaria sp, Celtis australis, Evonymus latifolia, Convulvulus (=Calistegia) sepium, Hedera pastochowii, Lamium album, Carex pendula, Rubus hyrcana, Ficus carica, Danae recemosa, Acer insigne, Parrotia persica, Carpinus betulus Cyclamen elegans, Marcantia* sp.

The water temperature of cave is 10-13°C (Mean 11.6°C) and is constant from the entrance to end of cave. Air temperature of cave varied between 12.5-21°C over six visits. The inside of the cave is a little warmer than the entrance of the cave (Table 2).

Locality 2. Vantakhteh. - The Spring of Vantakhteh (36° 40' N, 54° 25' E) is about 18 km south of Gorgan City and 5 km southwest of Ziarat Village at about 1200-1300 m elevation. Salamanders were observed in this locality in 1979 and later in Yakhkesh (2300 m elevation) on 25 November, 1999. There are two springs in this locality that are formed from soil and limestone and situated to east. Water flows from springs to the Souteh River.

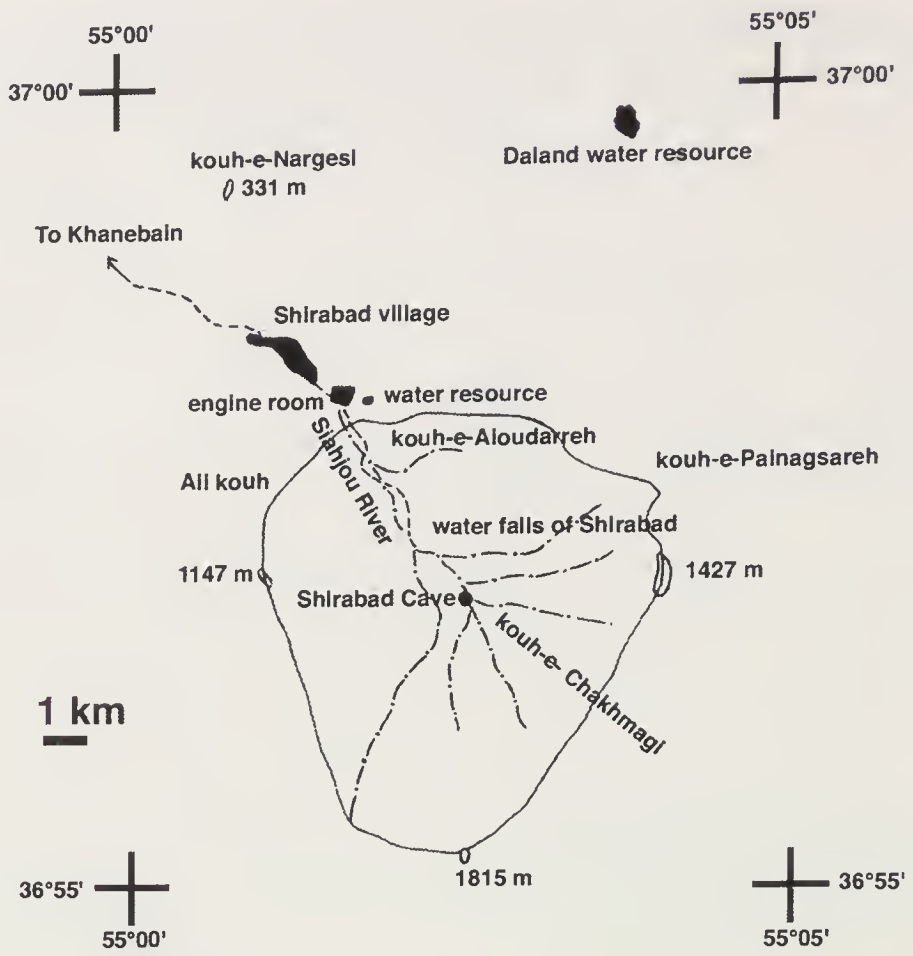

Figure 3. That National park that includes the cave and waterfalls of Shirabad (1650 Hectares).

The sides of the river were frozen and snowy. The springs are 3-4 m above the river. Water temperature of one spring was 6.5 and other 7°C. Air temperature was 6°C at 13:30 and 2°C at 15:30. Snow was melted in east side of the springs. Some plant species found around the springs are as follows: *Rosa albicans, Berberis vulgaris, Juniperus communis, Carpinus orientalis, Juncus effusus, Circium nekarmanicum, Stachys bizantica.* Five salamanders, all metamorphosed, were found inside of burrows near the springs.

Locality 3. Near Shirabad Cave. - Locality 3 is a small pond (about 2m x 2m) in southwest of Shirabad Village and 20 m above Shirabad Cave. Water depth was almost 50 cm. Around this shady pond were stones, lichens and trees (*Danae racemosa, Quercus* sp*)*. A Grass Snake (*Natrix natrix)*, Marsh Frogs (*Rana ridibunda)*, crabs (*Potamon* sp.*)* and larvae of *Batrachuperus persicus* with total length of 3-4 cm were observed. No adult or metamorphosed salamanders were seen. Air temperature was 20-23.5°C and water temperature was 19°C at 1000 on 10 July1997. Some larvae such as Gerridae (Heteroptera), Chironomidae (Diptera), Ephemeroptera, and Amphipoda (Gamaridae), earthworms (Lumbricidae), and Gastropoda were collected inside and around the pond under decaying logs.

Table. 3. Measurments of living *Batrachuperus persicus* inside of Shirabad cave of Golestan province of Iran. All specimens were released after measuring. All measurements are in mm.

Dateand number	Form	Total length	Head length	Trunk length	Tail length
1996/11/1n=6	larva	80	10	28.4	41.8
	larva	104.4	11.8	36.1	54.1
	larva	88.2	9.8	33.1	45.2
	larva	79.2	9.7	29.6	40.0
	larva	84.8	10.6	30.9	43.2
	adult	236.5	24.5	85	127
1997/2/28n=4	larva	70	-	-	-
	larva	83	-	-	-
	larva	79	-	-	-
	larva	74	-	-	-
1997/4/17n=4	larva	50	-	-	-
	larva	80	-	-	-
	adult	240	-	-	-
	adult	245	-	-	-
1997/7/10n=19	adult	229.2	26.6	78.6	124
	adult	227.7	24.8	81.9	121
	adult	-	29.3	84.2	-
	juvenile	97.3	11.9	37.5	48.6
	larva	45	-	-	-
	larva	57	-	-	-
	juvenile	90	-	-	-
	larva	80	-	-	-
	larva	86	-	-	-
	larva	62	-	-	-
	larva	52	-	-	-
	larva	50	-	-	-
	larva	67	-	-	-
	larva	56	-	-	-
	larva	103	-	-	-
	larva	108	-	-	-
	larva	94	-	-	-
	larva	55	-	-	-
	adult	217	-	-	-
1998/5/19n=13	larva	105	-	-	-
	adult	225	-	-	-
	adult	225	-	-	-
	adult	230	-	-	-
	adult	235	-	-	-
	larva	100	-	-	-
	larva	75	-	-	-
	larva	40	-	-	-
	larva	41	-	-	-
	larva	42	-	-	-
	larva	42	-	-	-
	larva	44	-	-	-
	larva	55	-	-	-
1999/4/26n=5	larva	37.9	-	-	-
	larva	36.8	-	-	-
	larva	36.2	-	-	-
	larva	36.9	-	-	-
	larva	75.5	-	-	-

Tab.4 . Morphometric and meristic characters of larvae and juveniles of *Batrachuperus persicus* in Golestan province of Iran.

ZMGU	Form	Total length	Head length	Head width	Head form	Upper eyelids	Between eyelids	Between nostrils	Trunk	Tail	Cloaca	Forelimb	Forelimb digits	Hindlimb	Hindlimb digits	Axilla-groin	Costal grooves
428	larva	38.5	6.6	-	rear wider	-	-	-	15.4	-	-	-	-	-	-	-	-
429	larva	38.7	-	-	rear wider	-	-	-	15.3	-	-	-	-	-	-	-	-
282	larva	39.2	6.6	8.4	rear wider	-	2.2	-	15	-	-	-	2>3>4=1	4.9	3>2=4>1	10.7	-
286	larva	40.1	6.8	7.6	rear wider	-	2.0	-	-	-	-	6.7	2=3>1>4	2.6		11.5	-
281	larva	40.4	6.1	7.6	rear wider	-	1.8	2	15.7	17.2	-	6.2	2>3>4=1	5.4	3>2>4>1	11.1	-
427	larva	42.0	6.6	6.5	rear wider	-	-	-	21.2	18.0	-	6.4	-	-	-	-	-
278	larva	42.3	7.3	7.8	rear wider	-	2.1	-	22.1	19.3	-	-	-	2.7		11.3	-
283	larva	51	7.4	9.8	rear wider	-	1.8	2.2	-	-	-	5.4	2>3>4=1	7.3	3>2>4>1	14.3	-
284	larva	55.1	8.0	9.5	rear wider	-	2.2	2.0	26.5	19.3	-	8.3	2>3>4>1	7.4	3>2>4>1	15.0	-
333	larva	75.5	-	-	rear wider	-	-		33.7	22.4	-	8.0	-	-	-	-	-
285	larva	-	10.6	12.1	rear wider	-	2.9	3.9	22.9	25	-	-	2>3>4>1	10.4	3>2>4>1	17.0	-
343	larva	84.8	10.8	11.0	rear wider	-	3.7	2.7	41.2	-	1.4	10.7	2=3>4=1	12.9	3>2>4>1	20.4	-
246	larva	-	12.3	11.3	rectangular	.9	2.5	4.1	32.1	-	0.9	11.8	3>2>4>1	11.5	3>2>4>1	16.8	12-12
248	larva	104.8	12.5	12.4	rectangular	1.5	3.2	4.2	35.9	40.3	2.4	11.5	3>2>4>1	16.2	3>2>4>1	30.1	12-11
430	juvenile	84.1	11.0	8.1	rear narrower	1.9	3.1	4	72.6	-	3.4	13.9	2>3>4>1	13.3	3>2>4>1	19.0	?-13
278	juvenile	102.1	14.8	10.9	rear narrower	2.8	3.1	3.9	15.4	51.1	4.1	12.9	3>2>4>1	16.6	3>2>4>1	22.5	-
276	juvenile	164.5	21.7	15.7	rectangular	3.9	4.5	6.0	15.3	41	4.5	13.8	3>2>4>1	28.2	3>4>2>1	51.1	13-14

Locality 4. Spring of Khouklou. - The Spring of Khouklou (36° 44' N, 54° 53' E) is situated almost 23 km south of Aliabad at about 1500 m elevation. This spring is 200 m west of Chenarbin and along side of the Khouklou River and situated to north beneath a large rock. This locality was studied on 26 May 1999. Six specimens were seen and three of them were collected. All specimens had external gills.

Materials and Methods

Shirabad Cave was studied 12 times and the other localities only one time between 1996 and 1999. Air and water temperature of the cave and two other localities measured on some dates. Important plant species of localities were identified. Measurements (total, head, trunk, and tail lengths) were done on living specimens of salamanders inside the cave. Some specimens (larval and transformed) collected and brought to aquaria at the zoology laboratory of Gorgan University and kept with ice. Some specimens (30) were fixed in alcohol or formalin. Almost all fixed transformed salamanders were dissected and stomach contents and sexes were noted. Morphometric and meristic characters of specimens were taken. The behavior of salamanders was studied inside the cave and in the laboratory. On each visit the total number of salamanders was counted from the entrance to the end of the cave.

Preserved specimens of *Batrachuperus persicus* studied for this research are as follows: ZMGU 67, 273, Shirabad Cave collected by H. Naghghash and M. Rahmani in 1994; ZMGU 246, 281, 282, 283, 284, near Shirabad Cave collected by H. Kami, A. Maghsoudlou, M. Rahmani, M. Azma on 10 July 1997; One specimen without number collected in Shirabad Cave by A. Maghsoudlou on 8 May 1998; ZMGU 267, Shirabad Cave, collected by A.Maghsoudlou on 21 May; ZMGU 266, 268, 269, 270, 272, 285, 286, 427, 428, 429, collected by H. Kami, M. Fatemi, N. Okhli, N. Moghaddam, J. Ghasemi, M. Mahmoudi, R. Zakeri, on 19 May 1998; ZMGU 275, 430, Shirabad Cave, probably collected by H. Kami, S. Afzali, R. Ghaemi on 28 February 1997; ZMGU 276, Jahannama Protected Area, south of Gorgan and Ziarat Spring of Khonakou, collected by N. Torbatinejad on 10 June 1997; ZMGU: 277, 278, Vantakhteh, collected by H. Kami, S. Afzali, M. Firouznia, H. Rezaee, Y. Shakoumahalli, Y. Nariman, on 25 November 1996; ZMGU 279, 280 without correct information (probably Vantakhteh or Shirabad); ZMGU 333, 335, Shirabad Cave, collected by M. Goli, S. Afzali and eight other students of Gorgan University on 27 April 1999; ZMGU 343, Spring of Khouklou, collected by H. Absalan, S. Hosseini, on 26 May1999.

Table 5. Morphometric and meristic characters of adult forms of *Batrachuperus persicus* in Golestan province of Iran (ZMGU 75 from Ardabil province, ZMGU 270 is dried specimen, rear narr =rear narrower, rear wid = rear wider, rectan = rectangular, F = Female, M = Male).

ZMGU	Total length	Head length	Head width	Head form	Upper eyelids	Between eyelids	Between nostrils	Trunk	Tail	Cloaca	Forelimb	Forelimb digits	Hindlimb	Hindlimb digits	Axilla-groin	Costal grooves	Sex
67	-	21.6	15.1	rear narr	4.1	4.5	5.4	86.5	-	5.9	25.0	2>3>1=4	26	3>2>4>1	41.9	11-12	M
335	93.3	25.3	18.9	rear narr	4.5	5.6	7.7	78.6	-	8.1	32.6	3>2>4>1		3>2>4>1	53.1	13-13	F
270	10.6	24.6	15.2	rear narr	3.5	5.3	6.4	72.4	89.4	-	-	3>2>1=4	-	-	-	11	-
-	23.2	24.9	18.6	rear wid	-	-	-	74	113.6	9.6	-	3>2>4>1	-	3>2=4>1	-	12-11	F
275	23.8	28.9	20.4	rectang	4.8	5.4	7.5	80.1	124.3	4.2	32.8	2=3>4>1	34.5	3>2>4>1	54.9	11-11	M
279	28.6	27.2	21.8	rear narr	3.8	5.9	7.1	82.8	114.8	7.5	29.9	2=3>4>1	37.1	3>4>2>1	57.7	13-12	F
273	29.2	26.7	19.2	rear narr	4.2	5.9	7.6	91.0	118.6	5.9	31.8	3>2>1=4	37.4	3>4>2>1	51.4	12-11	F
269	30.4	28.7	21.0	rectang	5.2	6.3	8.5	84.8	111.5	7.3	35.9	3>2>4>1	36.4	3>2>4>1	52.7	13-12	F
280	32.7	25.4	21.4	rectang	4.4	5.7	7.9	82.4	116.9	5.5	35.5	3>2>4>1	37.4	3>2>4>1	43.9	12-13	F
266	35.1	26.0	20.6	rear narr	-	5.5	7.8	88	124.9	5.9	37.3	3>2>4>1	39.7	3>2>4>1	59.0	14	M?
75	36.6	25.1	18.4	rectang	4.8	5.8	7.6	78.7	121.1	8.1	30.6	3>2>4>1	34.9	3>4>2>1	43.8	12-13	M
272	37.8	23.9	18.7	rectang	4.7	5.0	4.7	92.0	132.8	6.6	31.6	3>2>4>1	35.9	3>2=4>1	54.0	14-12	F
277	46.6	26.0	21.0	rectang	5.3	6.2	8.5	83.9	121.9	7.8	33.6	3>2>4>1	31.5	3>2>4>1	50/9	12-13	F
267	68.5	28.8	19.3	rear narr	5.1	6.1	8.3	90.6	136.7	6.3	34.6	3>2>4>1	-	3>2=4>1	-	13-11	F

Table 6. Summary of information on the feeding of *B. persicus* in Golestan province of Iran. ZMGU 75 is from Ardabil province.

ZMGU	Form	Total length	Stomach and intestine contents
267			Two hairless Bats (Myotis blythyii), one digested (~3 cm) and another undigested (~6 cm). Soft material is mixed with undigested bones in large intestine.
276	adult	268.5	One butterfly larva (chrysalid) 28 mm; ~45 vermiform larvae of Diptera (probably Tabanidae), each ~1 cm; two species of black beetle, (Coleoptera), ~45 mm; stomach of salamander was full.
277	adult	>164.5	Soft unidentifiable material.
75	adult	246.6	One larva of B. persicus with snout - vent length >32 mm, mostly digested.
	adult	236.6	Two mayfly larvae
333	adult	75.5	(Ephemeroptera). Specimen was fed on larvae of Iranian wood frog in laboratory before fixation.
335	adult	-	Some algae and a semidigested Earwig (Dermoptera) found in feces.
343	adult	84.8	Two undigested larvae of B. persicus with a total lenght of 30 mm emerged one day after collecting.

Results

Measurements of specimens from the localities are presented in Table 3. Morphometric and meristic characters of preserved salamanders are summarized in Table 4 and Table 5. The maximum total length of this species expected 15-20 cm (Schmidtler and Schmidtler 1971). The total length of the longest specimen was 268.5 mm.

Description of larvae. - In small larvae (Total length less than 80-100 mm), the head is large, depressed, more or less triangular with rounded end anteriorly, wider posteriorly, with small eyes and poorly developed eyelids; black horny margin present in lower jaw; gills large; vomerine tooth-bundle arc-shaped, situated anterolaterally, and extending in front of the choanae, short, in the middle hardly discernibly separated from one another. Trunk with 11-14 costal grooves, vertebral groove often present, forelimbs are longer than hind limbs, tips of fin-

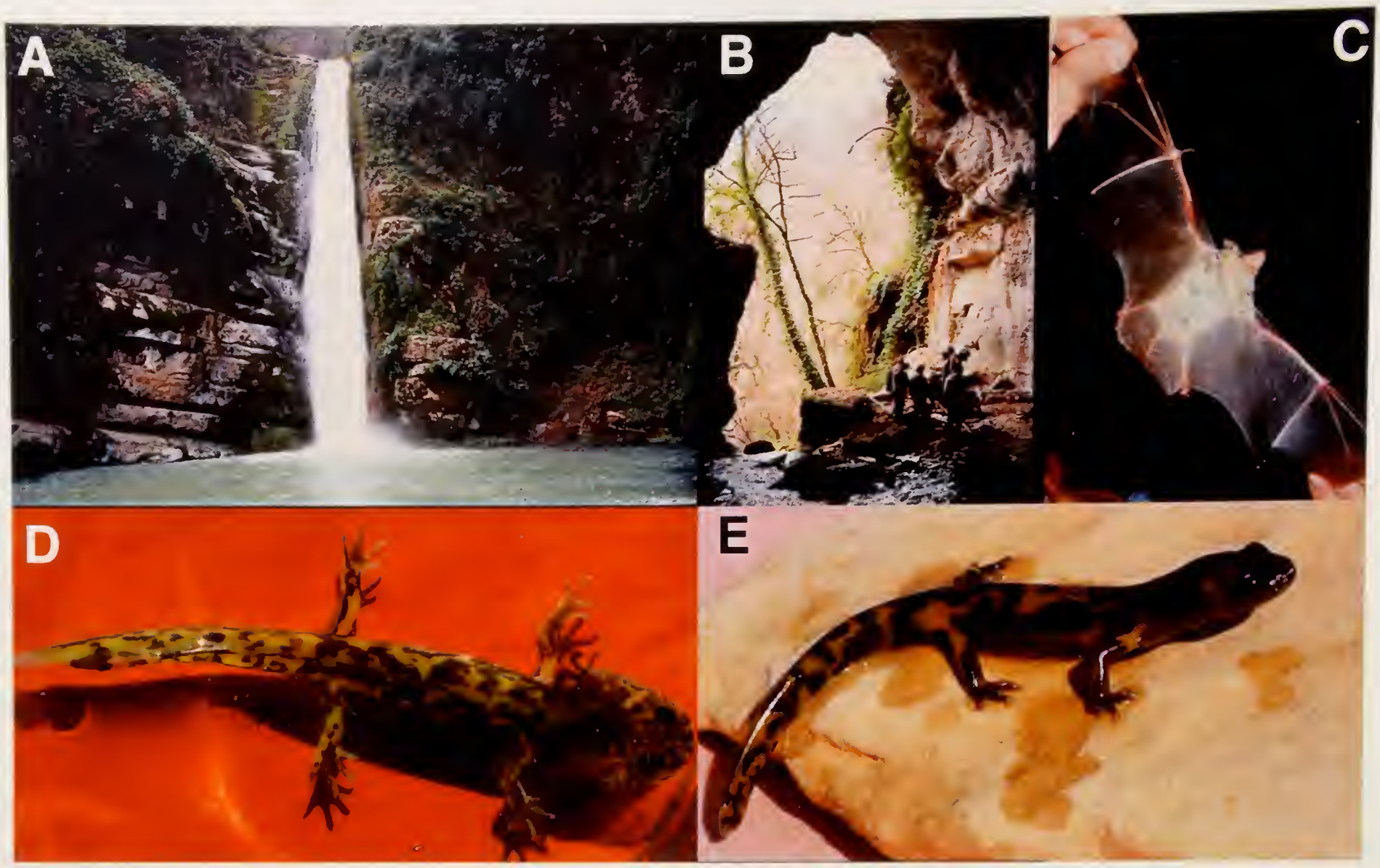

Figure 4. A- One of seven waterfalls of Shirabad Cave (Golestand Province, Iran). *Batrachuperus persicus* are found in the water near the edges of the pond (Photo by R. Ghaemi 2/28/97); B- The entrance of Shirabad Cave (Photo by R. Ghaemi 2/28/97); C- *Myotis blythyi*, an abundant bat species of Shirabad Cave and one of the food items of *Batrachuperus persicus*; D- Larval specimen of *Batrachuperus persicus* from Shirabad Cave collected 2/28/97 (Photo by A. Sanee 3/11/1997); E- Juvenile specimen of *Batrachuperus persicus* about 10 days after metamorphosis. Collected from Shirabad Cave 2/28/97 (Photo by A. Sanaee 4/8/97).

gers with black horny pads, their arrangements are 3>2>4>or<1; arrangement of toes are often 3>2>4>1; adpressed limbs not overlapping; tail highly compressed from laterally, upper caudal fin very distinct, reaching to occiput in some specimens, lower caudal fin reaching to posterior of cloaca, cloacal aperture is oval or elliptical. In larger larvae the head is more or less rectangular, adpressed limbs overlapping, upper and lower caudal fins not clearly distinct. The 12 larvae specimens examined (fixed or living) in this study (see Tables 3, 4) have a tail length which is smaller (Table 4) or longer (Table 3) than the head plus body length.

Description of juveniles. - Head more or less elliptical, decreasing toward the rear, adpressed limbs overlapping, upper and lower caudal fins are not distinct, tail more or less rounded especially at base of it. Four juvenile specimens examined in this study (see Tables 3, 4), have a tail length which is often smaller than the head plus body length.

Description of adults. - Head form is more or less rectangular, or wider anteriorly. Eyelids well developed and movable, width of eyelid is less than distance of intereyelids (interoculars), distance of external nostrils are longer than distance of nostril to anterior of eye, nostrils are semi-circle; vomerine tooth-bundle is different from that of larvae, inner portion of it is longer than outer one. Trunk with 11-14 costal grooves, adpressed limbs overlapping. Tail compressed laterally in some specimens and with thin upper and lower caudal fins, and in some specimens more or less rounded especially at base. Cloacal aperture is longitudinal and in some specimens cross-shaped, and longitudinal protuberance is present inside of cloaca in others. The 16 adult specimens examined in this study (see Tables 3, 5) have a tail length which is longer than head plus body length except two specimens (ZMGU 273, 335) which have tail lengths smaller than head plus body length.

Coloration. - Small larvae (Total length 40 mm) are in general light yellow without any distinct spots; dark eyes very distinct in small larvae, larger larvae have irregular dark gray spots, ventral portion of larvae light and without spots; dorsum of ZMGU 285 is dark gray; Iris yellowish, pupil dark, bases of all limbs yellow, yellow color of forelimbs not reaching to knee but in hindlimbs reaching to knee. Yellow spots of larvae are

more than in adults. Juveniles are darker than larvae. Yellow spots are less in adult, and ZMGU 269 is deep violet and have only one yellow spot beside of vertebral groove. Yellow spots of adults are often in vertebral groove.

Feeding. - *Batrachuperus persicus* feeds on larvae and adult forms of some orders of insects and probably other arthropods. They also feed on bats (*Myotis blythyi*)in Shirabad Cave (Fig. 4). Some specimens are cannibalistic and feed on smaller specimens of *B. persicus* especially in captivity. Algae, that may be eaten with other insects, was found in one larva. Stomach is white with a thin wall. Total length of digestive system of ZMGU 267 was 337 mm from anterior of stomach to posterior of cloaca. Contents of stomachs of some dissected *B. persicus* are shown in Table 6.

Behavior. - Small larvae and adult large salamanders are usually almost motionless inside of cave. They have no reaction to light. Adults escape to water. Adults swim more slowly than larvae under water. Adults are active in Shirabad Cave in all times of year but in other localities are not active during the daytime.

Parasites. - Many nematodes and mastigophorans were found inside the cloaca of one salamander from locality 2. Some nematodes moved freely and some were inside of a cyst.

Metamorphosis. - Larvae are found at all times of the year in Shirabad Cave and probably don't transform during the first year. A newly transformed juvenile was found on February 25 1997. Larvae transform rapidly in captivity probably as a result of starvation and higher temperature.

Habitat. - *Batrachuperus persicus* was studied in four localities and observed in some other localities in Golestan Province of Iran. Larvae were found inside of small shady ponds. Juveniles and adults were found inside and outside of water in Shirabad Cave but in other localities live in borrows about 20 cm long. Some specimens found above stones, and some in grooves of stones near water in Shirabad Cave. One specimen was 1 meter away of water and moved 0.5 meter on the stone which was in an almost vertical position.

Measurements. - Measurements are summarized in Tables 3, 4, and 5. Total length of the smallest larvae was 36.2 mm and of the longest one was 105 mm. Juveniles are smaller than the largest larvae. Total length of the longest adult was 268.5 mm.

Distribution. - *Batrachuperus persicus* collected or observed by students of Gorgan University, staffs of Department of Environment of Gorgan and Gonbad-e-Kavous, and by me in many localities in Golestan Province of Iran. These localities are listed on figure 2.

Discussion

These salamanders are active at all times of year in Shirabad Cave, but in other localities found in borrows of near of springs during daytimes and are probably active at night. Larval salamanders have morphological adaptations that correlate with the environments that the larvae inhabit (Noble 1927 in Petranka 1988). One dichotomy is that between species that typically breed in running versus standing water habitats. In this division larvae of *Batrachuperus persicus* are "stream-type" larvae. A third group of aquatic larvae ("mountain brook" larvae) was recognized by Valentine and Dennis (1964) that is perhaps better viewed as an extreme form of the stream-type morphology (Petranka, 1998). It is better recognized larvae of *B. persicus* to this type of larvae. Feeding on bats by adults of *B. persicus* may be unique in the world of salamanders.

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Editor's Note

The name *Batrachuperus persicus* Eiselt and Steiner, 1970. Ann. Naturhist. Mus. Wien, 74:77 (Holotype: NHMW 19435:4 [larval specimen], type locality: Talysch Mountains near Assalem, Gilan Province, Iran, small creek about 800 m) has priority over

Batrachuperus gorganensis Clerque-Gazeau and Thorn, 1979. Bull. Soc. Hist. Nat. Toulouse 114:455 (Holotype: MNHMP 1978-1982, type locality: At the edge of a cavernous stream on a clay bank 200 m inside the entrance of a cave, situated between the village of Gorgan and Ali-Abad, Elborz Mountain Range of north-central Iran, near the southeast shore of the Caspian Sea and with an elevation of 400 m above sea level). The type localities of the two nominal taxa lie at the extreme western and eastern ends respectively of the known Iranian range of *Batrachuperus*. Most recent authors have considered the two specimens conspecific and a small number of populations distributed between the two type localities have been discovered. However, the taxonomic status of *B. gorganensis* as well as that of intermediate populations remains unsettled. Unsettled; see also discussion of the problem in Ebrahimi et al. (2004). Indeed, Risch (1984, Alytes, Paris 3:44) made *B. gorganensis* the type of his monotypic genus, *Paradactylodon*. SCA

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Annotated Checklist of Amphibians and Reptiles of Pakistan

MUHAMMAD SHARIF KHAN

Apt # A17, 151-S. Bishop Ave., Secane, PA 19018, USA
E-mail: typhlops99@hotmail.com

Abstract. - From recent herpetological collections several new amphibian and reptilian taxa have been added to the herpetofauna of Pakistan. Thus raising the number of species from Minton's 144 and Mertens' 178 to 225.

Key words. - Checklist, Pakistan, herpetofauna.

Introduction

Following is the checklist of amphibian and reptile species that, so far, have been recorded and described in the major works on the herpetology of the subcontinent from the areas now included in Pakistan (Günther, 1864; Murray, 1884, 1886, 1892; Boulenger, 1890, 1896; Smith, 1931, 1935, 1943). Recently described and recorded species from Pakistan are also included in it (Anderson and Leviton, 1966, 1967, 1969; Anderson and Minton, 1963; Cherlin, 1981, 1983; Szczerbak, 1991; Golubev and Szczerbak, 1981; Ingoldby, 1922; Mertens 1969a,b, 1970, 1971, 1972, 1974; Baig, 1988, 1989, 1998, 1999; Baig and Böhme, 1996; Baig and Gvozdik, 1998; Dubois and Khan, 1979; Minton, 1966; Minton and Anderson, J. 1965; Minton et al., 1970; Khan, A. Q. and Khan, M.S. 1996; Khan, 1972, 1974, 1980, 1984a,b, 1988, 1989, 1991, 1992, 1993a,b, 1994, 1997a,b,c, 1998, 1999a,b, 2000, 2001a,b, 2003a,b; Khan and Baig, 1992; Khan and Khan, R.Z., 1997; Khan and Tasnim, 1989, 1990; Khan and Rösler, 1999; Rastegar-Pouyani, 1999.

Frogs and Toads

Family: Bufonidae

Bufo Laurenti, 1768

Bufo himalayanus Günther, 1864

Bufo latastii Boulenger, 1882

Bufo melanostictus hazarensis Khan, 2001

Bufo olivaceus Blanford, 1874

Bufo pseudoraddei pseudoraddei Mertens, 1971

Bufo pseudoraddei baturae Stock, Schmid, Steinlein, and Grosse, 1999

Bufo siacheninsis Khan, 1997

Bufo stomaticus Lütkin, 1862

Bufo surdus Boulenger, 1891

Bufo viridis zugmayeri Eiselt and Schmidtler, 1973

Family: Microhylidae

Microhyla Tschudi, 1828

*Microhyla ornata (*Duméril and Bibron, 1841)

Uperodon Dúmeril and Bibron, 1841

Uperodon systoma (Schneider, 1799)

Family: Ranidae

Euphlyctis Fitzinger, 1843

Euphlyctis cyanophlyctis cyanophlyctis (Schneider, 1799)

Euphlyctis cyanophlyctis microspinulata Khan, 1997

Euphlyctis cyanophlyctis seistanica (Nikolsky, 1900)

Hoplobatrachus Peters, 1863

Hoplobatrachus tigerinus (Daudin, 1802)

Fejervarya Bolkay, 1915

Fejervarya limnocharis (Boie, 1834)

Fejervarya syhadrensis (Annandale, 1919)

Nanorana Günther, 1836

Nanorana pleskei (Günther, 1896)

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Paa Dubois, 1975

Paa barmoachensis (Khan and Tasnim, 1989)

Paa hazarensis Dubois and Khan, 1979

Paa sternosignata (Murray, 1885)

Paa vicina (Stoliczka, 1872)

Sphaerotheca Duméril and Bibron, 1841.

Sphaerotheca breviceps (Schneider, 1799)

Turtles and Tortoises

Family: Cheloniidae

Caretta Rafiuesque, 1814

Caretta caretta (Linnaeus, 1758)

Chelonia Brongniart, 1800

Chelonia mydas (Linnaeus, 1758)

Eretmochelys Fitzinger, 1843

Eretmochelys imbricata (Linnaeus, 1766)

Lepidochelys Fitzinger, 1843

Lepidochelys olivacea (Eschscholtz, 1824)

Family: Dermochelyidae

Dermochelys Blainville, 1816

Dermochelys coriacea (Vandelli, 1761)

Family: Emydidae

Geoclemys (Gray, 1821)

Geoclemys hamiltonii (Gray, 1821)

Hardella Gray, 1870

Hardella thurjii Gray, 1870

Kachuga Gray, 1856

Kachuga smithii (Gray, 1863)

Kachuga tecta (Gray, 1831)

Family: Testudinidae

Agrionemys Khozatsky and Mlynarsky, 1966

Agrionemys horsfieldii (Gray, 1844)

Geochelone Fitzinger, 1835

Geochelone elegans (Schopff, 1792)

Family: Trionychidae

Aspideretes Hay, 1835

Aspideretes gangeticus (Cuvier, 1825)

Aspideretes hurum (Gray, 1831)

Chitra Gray, 1844

Chitra indica (Gray, 1831)

Lissemys Smith, 1931

Lissemys punctata andersoni Webb, 1980

Crocodiles and Gavials

Family: Crocodylidae

Crocodylus Laurenti, 1768

Crocodylus palustris Lesson, 1831

Family: Gavialidae

Gavialis Oppel, 1811

Gavialis gangeticus (Gmelin, 1789)

Lizards

Family: Agamidae

Brachysaura Blyth, 1856

Brachysaura minor (Hardwicke and Gray, 1827)

Calotes Cuvier, 1817

Calotes versicolor versicolor (Daudin, 1802)

Calotes versicolor farooqi Auffenberg and Rehman, 1995

Japalura Gray, 1853

Japalura kumaonensis (Annandale, 1907)

Laudakia Gray, 1845

Laudakia agrorensis (Stoliczka, 1872)

Laudakia badakhshana (Anderson and Leviton, 1969)

Laudakia caucasia (Eichwald, 1831)

Laudakia fusca (Blanford, 1876)

Laudakia himalayana (Steindachner, 1869)

Laudakia lirata (Blanford, 1874)

Laudakia melanura nasiri Baig, 1999

Laudakia melanura melanura Blyth, 1854

Laudakia microlepis (Blanford, 1874)

Laudakia nupta (de Filippi, 1843)

Laudakia nuristanica (Anderson and Leviton, 1969)

Laudakia pakistanica (Baig, 1989)

Laudakia pakistanica auffenbergi Baig and Böhme, 1996

Laudakia pakistanica khani Baig and Böhme, 1996

Laudakia tuberculata (Hardwicke and Gray, 1827)

Phrynocephalus Kaup, 1825

Phrynocephalus clarkorum (Anderson and Leviton, 1967)

Phrynocephalus euptilopus Alcock and Finn, 1896

Phrynocephalus luteoguttatus Boulenger, 1887

Phrynocephalus maculatus Anderson, 1872

Phrynocephalus ornatus Boulenger, 1887

Phrynocephalus scutellatus Olivier, 1807

Trapelus Cuvier, 1816

Trapelus agilis Olivier, 1804

Trapelus agilis agilis (Olivier, 1804)

Trapelus agilis pakistanensis Rastegar-Pouyani, 1999

Trapelus megalonyx Günther, 1864

Trapelus rubrigularis Blanford, 1876

Trapelus ruderatus baluchianus (Smith, 1935)

Family: Chameleonidae

Chamaeleo Laurenti, 1768

Chamaeleo zeylanicus Laurenti, 1768

Family: Eublepharidae

Eublepharis Gray, 1827

Eublepharis macularius (Blyth, 1854)

Family: Gekkonidae

Agamura Blanford, 1874

Agamura persica (Duméril, 1856)

Altigekko M.S. Khan, 2003

Altigekko baturensis (Khan and Baig, 1992)

Altigekko boehmei (Szczerbak, 1991)

Altigekko stoliczkai (Steindachner, 1869)

Bunopus Blanford, 1874

Bunopus tuberculatus Blanford, 1874

Crossobamon Boettger, 1888

Crossobamon lumsdeni (Boulenger, 1887)

Crossobamon maynardi (Smith, 1933)

Crossobamon orientalis (Blanford, 1876)

Cyrtopodion Fitzinger, 1843

Cyrtopodion agamuroides (Nikolsky, 1900)

Cyrtopodion kachhense kachhense (Stoliczka, 1872)

Cyrtopodion kachhense ingoldbyi Khan, 1997

Cyrtopodion kohsulaimanai (Khan, 1991d)

Cyrtopodion montiumsalsorum (Annandale, 1913)

Cyrtopodion potoharensis Khan, 2001

Cyrtopodion scabrum (Heyden, 1827)

Cyrtopodion watsoni (Murray, 1892)

Hemidactylus Oken, 1817

Hemidactylus brookii Gray, 1845

Hemidactylus flaviviridis Rüppell, 1835

Hemidactylus frenatus Schlegel, 1836

Hemidactylus leschenaultii Duméril and Bibron, 1836

Hemidactylus persicus J. Anderson, 1872

Hemidactylus triedrus (Daudin, 1802)

Hemidactylus turcicus (Linnaeus, 1758)

Indogekko M.S. Khan, 2003

Indogekko fortmunroi (Khan, 1993)

Indogekko indusoani (Khan, 1980)

Indogekko rhodocaudus (Baig, 1998)

Indogekko rohtasfortai (Khan and Tasnim, 1990)

Mediodactylus Szczerbak and Golubev, 1977

Indogekko walli (Ingoldby, 1922)

Ptyodactylus Goldfuss, 1820

Ptyodactylus homolepis Blanford, 1876

Rhinogecko de Witte, 1973

Rhinogecko femoralis (Smith, 1933)

Rhinogecko misonnei de Witte, 1973

Siwaligekko M. S. Khan, 2003

Siwaligekko battalensis (Khan, 1993)

Siwaligekko dattanensis (Khan, 1980)

Siwaligekko mintoni (Golubev and Szczerbak, 1981)

Teratolepis Günther, 1870

Teratolepis fasciata (Blyth, 1853)

Teratoscincus Strauch, 1863

Teratoscincus microlepis Nikolsky, 1899

Teratoscincus scincus (Schlegel, 1858)

Teratoscincus scincus keyserlingi Strauch, 1863

Tropiocolotes Peters, 1880

Tropiocolotes depressus Minton and J. A. Anderson, 1965

Tropiocolotes persicus persicus (Nikolsky, 1903)

Tropiocolotes persicus euphorbiacola Minton, S. Anderson, and J. A. Anderson, 1970

Family: Lacertidae

Acanthodactylus Wiegmann, 1834

Acanthodactylus blanfordii Boulenger, 1918

Acanthodactylus cantoris Günther, 1864

Acanthodactylus micropholis Blanford, 1874

Eremias Wiegmann, 1834

Eremias acutirostris (Boulenger, 1887)

Eremias aporosceles (Alcock and Finn, 1896)

Eremias fasciata Blanford, 1874

Eremias persica Blanford, 1874

Eremias scripta (Strauch, 1867)

Mesalina Gray, 1838

Mesalina brevirostris Blanford, 1874

Mesalina watsonana (Stoliczka, 1872)

Ophisops Ménétriés, 1832

Ophisops elegans Ménétriés, 1832

Ophisops jerdonii Blyth, 1853

Family: Scincidae

Ablepharus Fitzinger, 1823

Ablepharus grayanus (Stoliczka, 1872)

Ablepharus pannonicus (Fitzinger, 1823)

Chalcides Laurenti, 1768

Chalcides ocellatus (Forskål, 1775)

Eurylepis Blyth, 1854

Eurylepis taeniolatus taeniolatus (Blyth, 1854)

Lygosoma Hardwick and Gray, 1827

Lygosoma punctata (Linnaeus, 1766)

Mabuya Fitzinger, 1826

Mabuya dissimilis (Hallowell, 1860)

Mabuya macularia (Blyth, 1853)

Novoeumeces Griffith, Ngo, and Murphy, 2000

Novoeumeces blythianus (J. Anderson, 1871)

Novoeumeces indothalensis (M.S. Khan and M.R.Z. Khan, 1997)

Novoeumeces schneiderii zarudnyi (Nikolsky, 1900)

Ophiomorus Dúmeril and Bibron, 1839

Ophiomorus blanfordi Boulenger, 1887

Ophiomorus brevipes (Blanford, 1874)

Ophiomorus raithmai S. Anderson and Leviton, 1966

Ophiomorus tridactylus (Blyth, 1853)

Scincella Mittleman, 1950

Scincella himalayana (Günther, 1864)

Scincella ladacensis (Günther, 1864)

Family: Uromastycidae

Uromastyx Merrem, 1820

Uromastyx asmussi (Strauch, 1863)

Uromastyx hardwickii Gray, 1827

Family: Varanidae

Varanus Merrem, 1820

Varanus bengalensis (Daudin, 1802)

Varanus flavescens (Hardwicke and Gray, 1827)

Varanus griseus (Daudin, 1803)

Varanus griseus caspius (Eichwald, 1831)

Varanus griseus koniecznyi Mertens, 1954

Ophidia: Snakes

Family: Leptotyphlopidae

Leptotyphlops Fitzinger, 1843

Leptotyphlops blanfordii (Boulenger, 1890)

Leptotyphlops macrorhynchus (Jan, 1862)

Family: Typhlopidae

Ramphotyphlops Fitzinger, 1843

Ramphotyphlops braminus (Daudin, 1803)

Typhlops Oppel, 1811

Typhlops ahsanai M.S. Khan, 1999

Typhlops diardii Schlegel, 1839

Typhlops diardii platyventris M.S. Khan, 1998

Typhlops ductuliformes M.S. Khan, 1999

Typhlops madgemintonai madgemintonai M.S. Khan, 1999

Typhlops madgemintonai shermanai M.S. Khan, 1999

Family: Boidae

Eryx Daudin, 1803

Eryx conicus (Schneider, 1801)

Eryx johnii (Russell, 1801)

Eryx tataricus speciosus Zarevsky, 1915

Python Daudin, 1803

Python molurus (Linnaeus, 1758)

Family: Colubridae

Amphiesma Dúmeril, Bibron and Dúmeril, 1854

Amphiesma platyceps (Blyth, 1854)
Amphiesma sieboldii (Günther, 1860)
Amphiesma stolatum (Linnaeus, 1758)

Argyrogena Werner, 1924
Argyrogena fasciolata (Shaw, 1802)

Boiga Fitzinger, 1826
Boiga melanocephala (Annandale, 1904)
Boiga trigonata (Schneider, 1802)

Coluber Linnaeus, 1758
Coluber karelini karelini Brandt, 1838
Coluber karelini mintonorum Mertens, 1969

Enhydris Sonnini and Latreille, 1802
Enhydris pakistanica Mertens, 1959

Hemorrhois Boie, 1826
Hemorrhois ravergieri (Ménétriés, 1832)

Lycodon Boie, 1826
Lycodon aulicus aulicus (Linnaeus, 1758)
Lycodon striatus Shaw, 1802
Lycodon striatus bicolor (Nikolsky, 1903)
Lycodon striatus striatus (Shaw, 1802)
Lycodon travancoricus (Beddome, 1870)

Lytorhynchus Peters, 1862
Lytorhynchus maynardi Alcock and Finn, 1896
Lytorhynchus paradoxus (Günther, 1875)
Lytorhynchus ridgewayi Boulenger, 1887

Natrix Laurenti, 1768
Natrix tessellata (Laurenti, 1768)

Oligodon Boie, 1827
Oligodon arnensis (Shaw, 1802)
Oligodon taeniolatus (Jerdon, 1853)

Platyceps Blyth, 1860
Platyceps rhodorachis kashmirensis (M. S. Khan and A. Q.Khan, 2000)
Platyceps rhodorachis ladacensis (J. Anderson, 1871)
Platyceps rhodorachis rhodorachis (Jan, 1865)
Platyceps ventromaculatus bengalensis (M. S. Khan and A. Q.Khan, 2000)
Platyceps ventromaculatus indusai (M. S. Khan and A. Q. Khan, 2000)
Platyceps ventromaculatus ventromaculatus (Gray and Hardwicke, 1834)

Psammophis Fitzinger, 1826
Psammophis condanarus (Merrem, 1820)
Psammophis leithii leithii Günther, 1869
Psammophis lineolatus lineolatus (Brandt, 1838)
Psammophis schokari schokari (Forskål, 1775)

Pseudocyclophis Boettger, 1888
Pseudocyclophis persicus (J.Anderson, 1872)

Ptyas Fitzinger, 1843
Ptyas mucosus (Linnaeus, 1758)

Sibynophis Fitzinger, 1843
Sibynophis sagittarius (Cantor, 1839)

Spalerosophis Jan, 1865
Spalerosophis arenarius (Boulenger, 1890)
Spalerosophis diadema diadema (Schlegel, 1837)
Spalerosophis diadema atriceps (Fisher, 1885)
Spalerosophis schirazianus (Jan, 1865)

Telescopus Wagner, 1830

Telescopus rhinopoma (Blanford, 1874)

Xenochrophis Günther, 1864

Xenochrophis cerasogaster cerasogaster (Cantor, 1839)

Xenochrophis piscator piscator (Schneider, 1799)

Xenochrophis sanctijohannis (Boulenger, 1890)

Family: Elapidae

Bungarus Daudin, 1803

Bungarus caeruleus caeruleus (Schneider, 1801)

Bungarus sindanus razai M. S. Khan, 1985

Bungarus sindanus sindanus Boulenger, 1847

Naja Laurenti, 1768

Naja naja (Linnaeus, 1758)

Naja oxiana (Eichwald, 1831)

Family: Hydrophiidae

Astrotia Fisher, 1856

Astrotia stokesii (Gray, 1846)

Enhydrina Gray, 1849

Enhydrina schistosa (Daudin, 1803)

Hydrophis Latreille, 1802

Hydrophis caerulescens (Shaw, 1802)

Hydrophis cyanocinctus Daudin, 1803

Hydrophis fasciatus (Schneider, 1799)

Hydrophis lapemoides (Gray, 1849)

Hydrophis mamillaris (Daudin, 1803)

Hydrophis ornatus (Gray, 1842)

Hydrophis spiralis (Shaw, 1802)

Lapemis Gray, 1835

Lapemis curtus (Shaw, 1802)

Microcephalophis Lesson, 1834

Microcephalophis cantoris (Günther, 1864)

Microcephalophis gracilis (Shaw, 1802)

Pelamis Daudin, 1803

Pelamis platurus (Linnaeus, 1766)

Praescutata Wall, 1921

Praescutata viperina (Ph. Schmidt, 1852)

Family: Viperidae

Daboia Gray, 1842

Daboia russelii russelii (Shaw and Nodder, 1797)

Echis Merrem, 1820

Echis carinatus (Schneider, 1820)

Echis carinatus astolae Mertens, 1969

Echis carinatus multisquamatus Cherlin, 1981

Echis carinatus sochureki Stemmler, 1964

Eristicophis Alcock and Finn, 1896

Eristicophis macmahonii Alcock and Finn, 1897

Macrovipera Reuss, 1927

Macrovipera lebetina obtusa (Dwigubsky, 1832

Pseudocerastes Boulenger, 1896

Pseudocerastes bicornis Wall, 1913

Pseudocerastes persicus (Duméril, Bibron, and Duméril, 1854)

Family: Crotalidae

Gloydius Hoge and Romano-Hoge, 1981

Gloydius himalayanus (Günther, 1864)

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A Morphological and Taxonomic Study on *Lacerta parva* Boulenger, 1887 (Sauria: Lacertidae) from West Taurus, Turkey

Y. KUMLUTAŞ[1,*], S. H. DURMUŞ[1], Y. KASKA[2], M. ÖZ[3] AND M. R. TUNÇ[3]

[1]*Dokuz Eylül Üniversitesi, Buca Eğitim Fakültesi, Biyoloji A.B.D. Buca- İzmir,Turkey.*

[2]*Pamukkale Üniversitesi, Fen-Edebiyat Fakültesi, Biyoloji Bölümü Denizli-Turkey.*

[3]*Akdeniz Üniversitesi, Fen-Edebiyat Fakültesi, Biyoloji Bölümü Antalya-Turkey.*

[*]*To whom correspondence should be addressed E-mail: yusuf.kumlutas@deu.edu.tr*

Abstract. - The morphometric measurements of taxonomically important characters, coloration, and pholidosis features of 74 *Lacerta parva* specimens collected from West Taurus, Turkey were investigated. Statistical analyses were done and these results were compared with those from relevant literature. Some of the characters were found to be different on the specimens from different localities. New localities from southwest Turkey were also discovered during this study.

Key words. - *Lacerta parva,* West Taurus, Turkey.

Introduction

Lacerta parva was first identified as a new species based on a female specimen collected from Kayseri, Turkey (Boulenger, 1887). In later studies, the distribution of this species was extended to include all of Anatolia and the Caucasian region (Werner, 1902; Nesterow, 1912; Nikolsky, 1915; Bird, 1936; Bodenheimer, 1944; Mertens, 1952; Başoğlu and Baran, 1977; Baran et al., 1992; Baran and Atatür, 1998). The distribution of this species was extended to Europe by giving the locality from Tekirdağ, Turkey (Venchi-Bologna, 1996).

Peters (1962) compared the variations and similarities between Caucasian and Anatolian populations by examining the 131 and 74 specimens, respectively. Atagün (1984) also did a comparative study on the 208 specimens collected from six different sub-populations (Fethiye, Denizli, Konya, Ankara, Kayseri, Erzurum) from Anatolia. Recently, Mülayim et al. (2001) studied 46 specimens collected from Gölkaşı Village, Beyşehir-Konya and found much more similarities between Konya and Fethiye populations as previously mentioned by Atagün (1984).

This work investigates the distribution of this species in the west of Turkey and also provides morphometrical comparison of these specimens with previously collected specimens and relevant literature. We try to resolve the taxonomical situation of the sub-populations of *Lacerta parva* in Anatolia.

Material and Methods

Most of the specimens were obtained from Taurus, southwest of Anatolia. A sum of 22 male, 38 female and 14 juvenile specimens were collected. These specimens, collected during the years of 1995-1997, were kept at ZDEU (Zoology Department of Ege University). The locations where the samples were collected are given in Figure 1. The list of material is given below as the Departmental Identification Code, sex, number of specimens, locality, date, initials, and surname of the collectors respectively.

List of Material

1) 140 / 1995, 1 male, Beyşehir, 19.09.1995, Leg. M. Öz.
2) 238 / 1996 1-9 males, 10-22 females, Bozhöyük Ovacık-Elmalı, 18.06.1996, Leg. Y. Kumlutaş , R. Tunç, S. H. Durmuş.
3) 239 / 1996, 1-5, 6-13, 14-27 Juv., Çayryakas - Gazipaşa, 23.08.1996, Leg. Y. Kumlutaş, M. Öz, R. Tunç.
4) 163 / 1997, 1-7, 8-24 , Beyobası, 25.06.1997, Leg. Y. Kumlutaş, M. Öz, R. Tunç.

Coloration of living specimens was determined by eye, slides were taken, and then the specimens fixed with the traditional processes and kept in 70% alcohol. The morphometric measurements were done with a digital calliper with an accuracy of 0.02 mm. The body Measurements taken and their descriptions and indexes of the characters are as follows. **Pileus Width (PW):**

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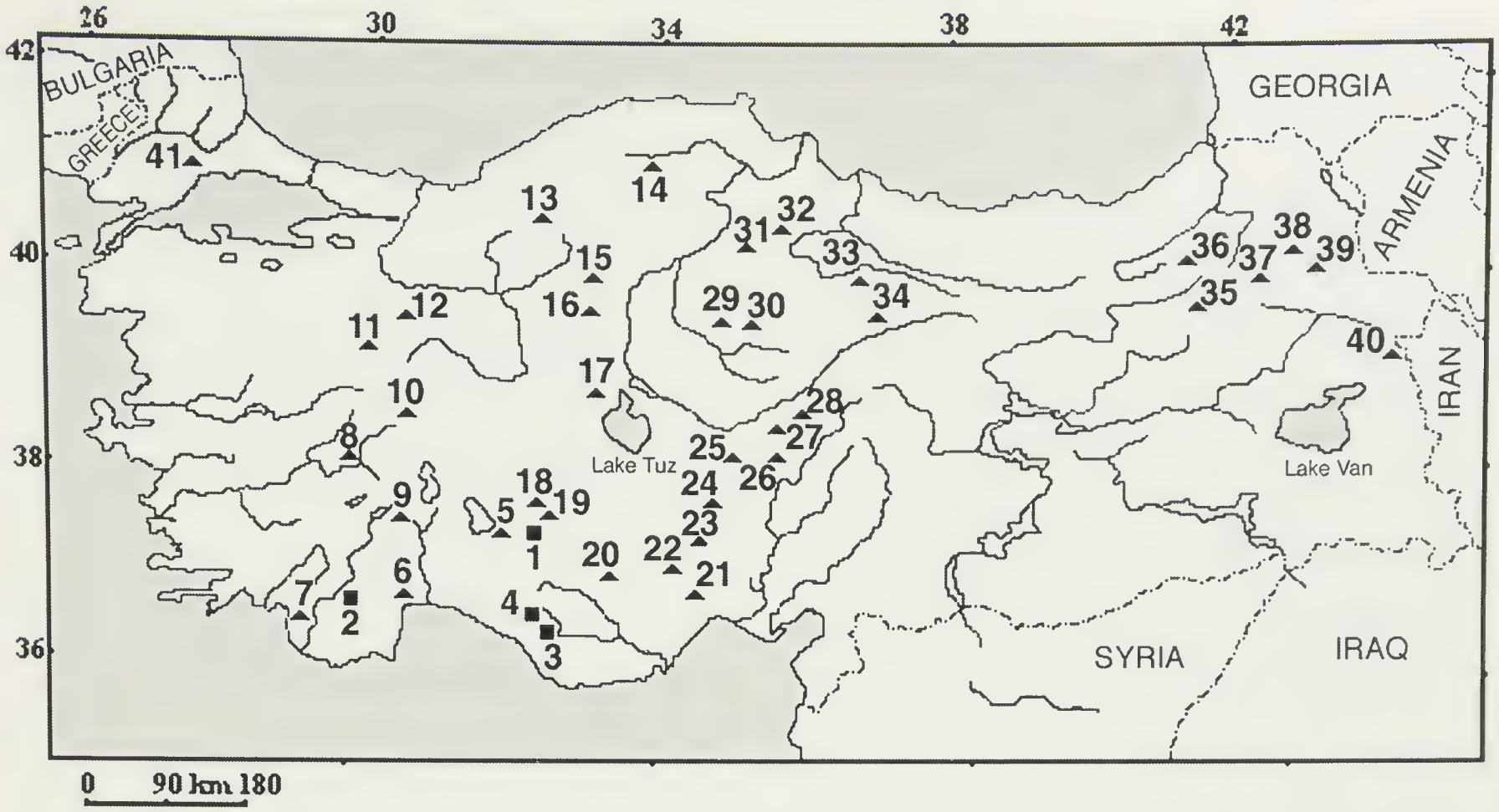

Figure 1. The distribution of *Lacerta parva* in Turkey.

■: Collection localities in this study. Refer to the materials list for details.

▲: Collection localities from literature (Peters, 1962; Atagün, 1984; Başoğlu-Baran, 1977; Baran et al., 1992; Venchi-Bologna, 1996; and Mülayim et al., 2001).

1- Beyşehir-Konya (30 km)
2- Bozhöyük-Ovacık
3- Çayıryakası-Gazipaşa
4- Beyobası
5- Gökkaşıköyü-Beyşehir
6- Antalya
7- Fethiye
8- Akdağ-Çivril
9- Isparta
10- Afyon
11- Kütahya
12- Eskişehir-Alayurt arası
13- Gerede
14- Kastomonu
15- Çubuk-Ankara
16- Ankara
17- Kulu-Konya
18- İnevi-Konya
19- Konya
20- Karaman
21- Dümbelek Mount-Mersin
22- Akgöl
23- Ulukışla
24- Niğde
25- Niğde-Kayseri arası
26- Erciyes Dağı
27- Kayseri
28- Bünyan-Kayseri
29- Yozgat
30- Sorgun-Yozgat
31- Between Mecitözü and Çorum
32- Suluova-Amasya
33- Tekneli Village-Tokat
34- Akdağ-Sivas
35- Erzurum
36- Akdağ (Northeast Anatolia)
37- Horosan-Erzurum
38- Sarıkamış
39- Kağızman
40- Between Culfa and Lake Van
41- Tekirdağ

The widest distance between the parietal plates. **Pileus Length (PL):** The distance from the posterior point of parietal plates to the tip of rostrum. **Head and Body Length (HBL):** The distance between the front tip of rostrum and front edge of anus. **Body Length (BL):** The total length of body from tip of rostrum to the end of tail. **Tail Length (TL):** The length of tail from anus to the tip of tail. **Forelimb Length (FL):** The length of forelimb from the body connection to the tip of longest finger. **Hind-limb Length(HL):** The length of hind limb from the body connection to the tip of fourth finger. **Pileus Index (PI)**=PW/PLx100, **Tail Index (TI)**=TL/BLx100 and **Forelimb Index (FI)**=FL/BLx100 were also calculated. The ANOVA statistical test were used in comparison of the measurements and the ratios (Minitab, 1991). The values of "Coefficient of difference (CD)" were used in comparison of some characteristics among the population (Mayr, 1969).

Results

Pholidosis and Morphometric Measurements

Table 1: The results of descriptive statistics on some of the characteristics of *L. parva* specimens (These measurements are given as milimeter).

Parameter		N	Mean (Min –Max)	SD	SE
Pileus Width (PW)		60	5.28 (4.38-6.90)	0.48	0.06
Pileus Length (PL)		60	10.31 (8.72-11.76)	0.74	0.09
Head and Body Length (HBL)		60	49.84 (42.12-58.81)	3.41	0.44
Tail Length (TL)		32	74.34 (53-96)	10.50	1.87
Pileus Index (PI)		60	51.17 (44.78-60)	2.17	0.28
Tail Index (TI)		29	60.32 (51.36-65.14)	3.25	0.60
Forelimb Index (FI)		59	29.70 (24.81-34.58)	2.34	0.30
Supra-cilliar Granule		74	6.24 (1-10)	2.03	0.24
Supra-cilliar Plate		74	5.36 (4-9)	0.76	0.08
Median Gularia		74	17.61 (15-19)	1.16	0.13
No. of Lateral Lines in Ventralia	male	22	28.27 (27-30)	0.94	0.20
	female	38	31.90 (28-34)	1.13	0.18
	male+female+Juv	74	30.47 (27-34)	2.08	0.24
Dorsalia		74	37.13 (33-43)	1.94	0.22
Femoral Opening	male	22	17.23 (14-26)	2.47	0.53
	female	38	15.95 (14-18)	1.31	0.21
	male+female+Juv	74	16.16 (14-20)	1.36	0.16
No. of 4. Sub-digital Lamellae		74	20.52 (17-23)	1.11	0.13

Rostrale were connected to the nostril and the numbers of postnasal plate were occasionally two (96%), only one (3%) in two specimens and one specimen had one on the left and two on the right. The number of occipital plates were also commonly one (97%) but divided into two in two (3%) specimens. The numbers of superciliary plates was five in 44 specimens (59.4%), six in 23 specimens (31.1%), four in four specimens (5.4%), seven in two specimens (2.7%) and nine in one specimen (1.4%). The numbers of supralabial plates, in front of the subocular plate, was usually four (74.3%); three in two specimens (2.7%); four (one small and three big) in three specimens (4.05%); five in two specimens as two small and three big ones; four big and one small in six (8.1%) other specimens; six (four big and two small) in two specimens, seven (four big and three small) in two specimens. The distal end of the collaria was jagged in shape and the numbers varied between five and eight with a mean of 6.7. The results from statistical analyses of the above mentioned measurements are presented in Table 1; comparative results with other literature are presented in Table 2. There were no statistical differences (F-test, $P>0.05$) between the specimens collected from different locations in this study.

Although the T-test does not show any statistical differences ($P>0.05$) between males and females, males have relatively higher values than females. For example, the mean length of the pileus was 11.15 (Min.= 9.64 - Max.=16.60) in males and 9.99 (8.72 - 11.50) in females. The coefficient of differences (CD) was 0.59. The width of the pileus was 5.53 (4.74 - 6.23) in males and 5.14 (4.38 - 6.90) in females and the CD was 0.44.

Table 2: The comparison of some of characters between the populations of *L. parva* from Fethiye, Denizli, Konya, Ankara, Kayseri, Erzurum and Beyehir with samples collected from Taurus.

Parameter	Fethiye specimens (Atagün, 1984)		Denizli specimens (Atagün, 1984)		Konya specimens (Atagün, 1984)		Ankara specimens (Atagün, 1984)		Kayseri specimens (Atagün, 1984)		Erzurum specimens (Atagün, 1984)		Beyehir specimens (Mülayim etal , 2001)		Taurus specimens (In this study.)	
	N	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**
Dorsalia	12	36,58	28	37,96	24	39,04	55	37,85	74	38,45	15	35,86	46	36,70	74	37,13
Femoral Opening	11	15,54	28	15,79	24	16,79	55	15,80	74	16,64	15	16,13	46	15,63	74	16,16
4. Subdigital Lamellae	12	20,75	28	21,93	24	21,21	54	21,06	74	21,38	15	19,73	46	20,52	74	20,52
Supracilliar Granule							55	7,25			15	8,93	46	6,76	74	6,24
Median Gularia	12	17,50			24	19,13							46	16,67	74	17,61
Ventralia No. of lateral plate													46	29,98	74	30,47
HBL													46	48,04	60	49,84

The tail was longer in males (76.59) than females (70.62) and the CD of this measurements was 0.28.

Color and Pattern. - Dorsal coloration is more ground, grayish-brown in the Elmalı population and lighter brown in the other three populations studied. A slim dark line was present from posterior of occipital scute towards the posterior. This line does not stretch to the base of forelimbs in juveniles. There were few dark spots on the vertebrals of some specimens (11%). Dark blotches extending dorsoventrally from vertebal line formed bands, particularly on Beyobası specimens. The supra-temporal line was usually continuous until the middle part of body; broken lines continued posteriorly to the base of the tail or sometimes until the tip of tail in some specimens. Small spots are present, their central parts are greenish-blue and surrounding areas are dark starting at the base of the forelimb and usually continuing posteriorly. The subocular line is dirty white in color and continues to the hindlimbs. Dark spots were present under this line in some specimens.

Ventral scales are yellow in males, especially during the breeding season (which change to white later in the season), and lighter in females. However, the color under the hind limb was sometimes yellowish; the other parts were pinkish-white for females. Dark stains on ventralia were absent on the samples, except for the last ventral plate.

Ecological Observations. - The three specimen collection localities were new localities for *L. parva*, except for the Beyşehir population. These habitats were nearly 2000 m in altitude (i.e., Bozhöyük-Ovacık 1800 m., Çayıryakası-Gazipaşa 1850 m.,

Beyobası 1900 m.). The 22 specimens, from Bozhöyük-Ovacık population, were caught between bushes and small vegetation. The weather was a bit cloudy and the temperature was approximately 24°C. *Laudakia stellio* and *Ablepharus kitaibelii* species were also observed in the same habitat. The specimens from Çayıryakası and Beyobası were caught while active or under stones at the temperature around 29°C. The collection habitats of the specimens were covered mainly small bushy vegetation not big trees. *Lacerta danfordi*, *Mabuya vittata*, *Cyrtopodion kotschyi* and *Natrix natrix* species were also observed in the same area.

Evaluation and Discussion

There were no statistical differences between the different populations in this study, but tail length, pileus length, fore-limb and hind-limb lengths, and the number of femoral openings were higher in males than females.

The head and body length and the number of lateral plate lines were higher in females than males. Atagün (1984) reported that only one plate is present behind the postnasal plate in 26% of the specimens from the Erzurum population, but not present in the remaining five populations in his work. We did not record any such character from our specimens. Atagün (1984) also reported that the division of the occipital plate was also different in the Erzurum population by having a higher number of divisions. This population was also studied by Peters (1962), but he did not mention such differences. Only a small percent (3%) of our specimens showed a division in the occipital plate.

Peters (1962), in his study comparing *L. parva* populations between Caucasia and Anatolia, found that the mean number of dorsalia were different (males = 35.97; females = 34.76) in Caucasian population than Anatolian population (males= 38.52; females= 37.53). Our values from West Taurus (males= 37.68; females= 36.42) were very similar to Peters (1962) values from Anatolia. This value, along with other parameters, are presented in Table 2. As it can be seen from this table, the results of this work are very close to the results of the Beyşehir population reported by Mülayim et al. (2001).

Peters (1962) also reported the mean number of lamellae under the fourth finger to be very similar between the Caucasian (males= 21.6; females= 21.2) and Anatolian (males= 22.6; females= 22.1) specimens. Our results for this character were slightly lower than Peters' results but very close to the results of Mülayim et al. (2001) (Table 2). The number of femoral openings reported by Peters (1962) were slightly higher (males= 17.56; females= 16.46) for Caucasian than for Anatolian (males= 17; females= 15.91) specimens. The number of femoral openings in this study were found to be very close to the most eastern Anatolian population of Erzurum (Table 2). The HBL, the mean numbers of supracilliar plate, lateral plates in ventralia were very similar with the results of Mülayim et al. (2001), but the mean number of median gularia in this study was very close to the Fethiye population reported by Atagün (1984). There were no remarkable differences in color and pattern reported by others (Peters, 1962; Atagün, 1984; Baran et al., 1992; Mülayim et al., 2001) and our results.

As it can be seen from our present and other previous studies, phenotypic variation among the reptile populations from Turkey have been quantified extensively using morphological characters. Comparison of morphometric measurements may yield a new subspecies, but the different populations of *L. parva* from Turkey may vary even genetically. Unfortunately, genetic diversity at the intra-specific level is not available for any species in Turkey. Sequencing DNA, in particular mtDNA, may help to solve the taxonomic problems present in the herpetofauna of Turkey, as it was done for other amphibian species (i.e. Garcia-Paris et al., 1998) and for sea turtles (i.e., Bowen et al., 1994; Kaska, 2000).

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Genetic Variation Among Agamid Lizards of the *Trapelus agilis* Complex in the Caspian-Aral Basin

J. Robert Macey[1,2,*] and Natalia B. Ananjeva[3]

[1]*Department of Evolutionary Genomics, Joint Genome Institute, Lawrence Berkeley National Laboratory, 2800 Mitchell Drive, Walnut Creek, CA 94598-1631, USA*

[2]*Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA*

[3]*Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia*

**To whom correspondence should be addressed: E-mail: jrmacey@lbl.gov*

Abstract. - Allozyme variation is examined in eight populations of *Trapelus* from the Caspian-Aral Basin of the former USSR. Thirty one loci (15 variable) exhibit remarkably low levels of genetic variation with only a Nei's genetic distance of 0.117 across 2500 km. An isolated population on the European side of the Caspian Sea is found to phenetically cluster inside the Asian populations examined, suggesting that it should not be considered taxonomically distinct.

Key words. - Reptilia, Squamata, Agamidae, *Trapelus*, Central Asia, biogeography, allozyme electrophoresis.

Introduction

The *Trapelus agilis* complex is distributed on the Iranian Plateau and adjacent regions of southwestern Asia, as well as in the Caspian-Aral Basin to the north in the interior of Asia. Two separate populations of the *Trapelus agilis* complex are separated by the Caspian Sea in the Caspian-Aral Basin (including regions draining to Lake Balkhash) of the former USSR. One population on the eastern side of the Caspian Sea ranges from western China, Kazakhstan, and Kirgizistan in the north, to Turkmenistan (Fig. 1), Uzbekistan, and Tadjikstan in the south. This Central Asian population is continuous with Iranian, Afghan, and other southwest Asian populations referred to *Trapelus agilis*. On the western side of the Caspian Sea in Europe a small population occurs in Chechenia and Dagestan, Russia. The two populations occurring in the Caspian-Aral Basin are placed either in a separate species, *T. sanguinolentus,* or subspecies, *T. agilis sanguinolentus*. Taxonomic controversy also exists as to the status of the isolated European population of *Trapelus*. Some authors consider the European population to be a distinct subspecies of *T. sanguinolentus* (*T. s. sanguinolentus*) with the Central Asian populations being referred to *T. s. aralensis* (Ananjeva and Tsaruk, 1987). Others consider the European and Asian populations in the Caspian-Aral Basin to be a single taxon, either *T. sanguinolentus* (Bannikov et al., 1977) or *T. agilis sanguinolentus* (Wermuth, 1967). The focus of this study is on the relative position of the European and Asian populations in the Caspian-Aral Basin. The Caspian-Aral Basin populations are always grouped together either as a species or as one or two distinct subspecies relative to the southwest Asian populations referred to as *T. agilis*.

Trapelus is an old genus of Agamid lizards with an Afro-Arabian origin (Macey et al., 2000b). Sequence divergence between *Trapelus* species in Africa (*Trapelus savignii*), Arabia (*T. persicus*), the Iranian Plateau (*T. agilis*), and the Caspian-Aral Basin (*Trapelus sanguinolentus* population 6 of this study), which form a clade, is 10.7-13.9% for the mitochondrial DNA segment spanning from *nad1* to *cox1* (Macey et al., 2000b). Applying the rate of 1.3% change per million years for pairwise comparisons as calculated for this segment of mitochondrial DNA in agamid lizards of the genus *Laudakia* (Macey et al., 1998), divergence times among these species of *Trapelus* are estimated to be 8.3 to 10.7 million years before present (MYBP). These data suggest that the genus has been in Asia since the Miocene.

Allozyme data are used to distinguish hypotheses of early divergence of the European and Asian trans-Caspian populations into discrete entities, verses colonization of the European side of the Caspian Sea by western Asian populations. High mountains in the Caucasus and Elburz ranges prevent colonization of the European population from the south, where a continuous land connection does exist to *Trapelus* populations in Iran. The Caspian-Aral Basin corresponds to much of the Paratethys Sea, which during the Miocene almost completely dried up 5-6 MYBP and then returned briefly in the Pliocene, 3.0-3.5 MYBP (Steininger and Rogl, 1984). Divergence following the early period (5-6 MYBP) when much of the Caspian-Aral Basin was

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Figure 1. A *Trapelus* from Repetek Desert Reserve Station, Repetek (38° 34' N, 63° 11' E), Chardjou Region, Turkmenistan. The photo was taken in May, 1989. This is a representative of population 5 of this study.

available for colonization, should halt gene flow in the late Miocene or Pliocene and two discrete populations are expected to be detected, one in Europe and one in Asia. Alternatively, a more recent colonization from a founder event, when the Caspian Sea level fluctuated in the Pleistocene, should have a much later restriction in gene flow and therefore the European population may be expected to be nested within the Asian population.

Material and Methods

Laboratory Protocols. - Tissues were taken in the field, immediately frozen in liquid nitrogen, and later transferred to an ultracold freezer and maintained at -80° C. For analysis of allozymic variation, liver and muscle tissues were homogenized separately. Horizontal starch-gel electrophoresis was employed to differentiate variation in 31 presumptive loci. The 31 loci and eight buffer conditions utilized to resolve them are displayed in table 1. Allozymes were stained using standard methods (Harris and Hopkinson, 1976; Murphy et al., 1990; Richardson et al., 1986; Selander et al., 1971). Carboxylic ester hydrolase (Dimeric Esterase) was resolved using 4-methylumbelliferyl acetate as the substrate, Alcohol dehydrogenase (ADH) was resolved using *Trans*-2-Hexen-1-ol as the substrate, an unidentified peptidase (PEP-1) was resolved using L-leucyl-L-alanine as the substrate, and Peptidase D (PEP-D) and an unidentified peptidase (PEP-2) with the use of L-phenylalanyl-L-proline as the substrate. The isozymes, and loci if more than one, were labeled according to their migration from anode to cathode.

Specimen Information. - Museum numbers and localities for voucher specimens are presented below. Acronyms are CAS for California Academy of Sciences. San Francisco and MVZ for Museum of Vertebrate Zoology, University of California at Berkeley. Russia: (population 1) Tersko-Kumskaya nizmennast (the lowland between Terek and Kuma Rivers), 15 km WNW (airline) of Voskresenskaya, which is approx. 25 km NNW of Gudermes (43° 21' N 46° 06' E), Schelkovskaya District, Chechen-Ingush Autonomous Republic (CAS 182952, 183032-183038). Kazakhstan: (population 2) Almaty (43° 15' N 76° 57' E), Almaty Region (MVZ 216014-216016, CAS 183047-183051). Uzbekistan: (population 3) sand dunes on the west side of the Surkhan Darya (River), on the Kumkurgan (37° 48' N, 67° 37' E) to Denau (38° 16' N, 67° 54' E) Rd., Surkhan Darjinskaya Region (CAS 183004-183006).

Table 1. The 31 protein loci scored and the electrophoretic conditions within which they were resolved.

Enzyme or blood protein	Electrophoretic abbreviation	E. C. No.	No. of Loci	Tissue[a]	Conditions[b]
Serum albumin	AB	-	1	L	1
Aconitase hydratase	ACON	4.2.1.3	1	L	2
Adenylate kinase	AK	2.7.4.3	1	M	2
Alcohol dehydrogenase	ADH	1.1.1.1	2	L	3
Aspartate aminotransferase	AAT	2.6.1.1	1	L	4
Carboxylic ester hydrolase	EST-D[c]	3.1.1.-	2	L	1
Creatine kinase	CK	2.7.3.2	1	M	4
Fructose-bisphosphate aldolase	FBA	4.1.2.13	2	L	5
Glucose-6-phosphate isomerase	GPI	5.3.1.9	2	L	4
Glycerol-3-phosphate dehydrogenase	G3PDH	1.1.1.8	1	L	1
D-2-Hydroxy-acid dehydrogenase	HADH	1.1.99.6	1	L	5
L-Iditol dehydrogenase	IDDH	1.1.1.14	1	L	5
Isocitrate dehydrogenase	IDH	1.1.1.42	2	L	2
L-Lactate dehydrogenase	LDH	1.1.1.27	2	L	3
Malate dehydrogenase	MDH	1.1.1.37	2	L	6
Mannose-6-phosphate isomerase	MPI	5.3.1.8	1	L	6
Peptidase (unidentified 1)	PEP-1	3.4.-.-	1	L	1
Peptidase D	PEP-D	3.4.13.9	1	L	7
Peptidase (unidentified 2)	PEP-2	3.4.-.-	1	L	7
Phosphoglucomutase	PGM	5.4.2.2	1	L	8
Phosphogluconate dehydrogenase	PGDH	1.1.1.44	1	L	6
Purine-nucleoside phosphorylase	PNP	2.4.2.1	1	L	7
Pyruvate kinase	PK	2.7.1.40	1	L	8
Superoxide dismutase	SOD	1.15.1.1	1	L	4

[a]Tissue abbreviations are: L = liver; M = skeletal muscle.
[b]Electrophoretic conditions: (1) Lithium-borate/Tris-citrate pH 8.2, 250 v for 6 h (Selander et al., 1971); (2) Amine-citrate (Morpholine) pH 6.0, 250 v for 6 h (Clayton and Tretiak, 1972); (3) Tris-citrate/borate pH 8.7, 250 v for 5 h (Selander et al., 1971); (4) Histidine-citrate pH 7.8, 150 V for 8 hours (Harris and Hopkinson, 1976); (5) Phosphate-citrate pH 7.0, 120 v for 7 h (Selander et al., 1971); (6) Tris-citrate II pH 8.0, 130 v for 8 h (Selander et al., 1971); (7) Tris-HCL pH 8.5, 250 v for 4 1/2 h (Selander et al., 1971); (8) Tris-maleate-EDTA pH 7.4, 100 v for 10 h (Selander et al., 1971).
[c]EST-D = Dimeric Esterase

Turkmenistan: (population 4) SW bank of the Amur Darya (River), approx. 2 km NE of Nephtezavodsk which is 30 km WNW of Deynau (39° 15' N, 63° 11' E), Chardjou Region (CAS 179552-179559); (population 5) 1 km north of Repetek Desert Reserve Station, Repetek (38° 34' N, 63° 11' E), Chardjou Region (CAS 179199-179203, 179416-179420), and Repetek Desert Reserve Station, Repetek (38° 34' N, 63° 11' E), Chardjou Region (CAS 179331); (population 6) 55 km north of Ashgabat (37° 57' N, 58° 23' E) on the Ashgabat - Bakhardok (38° 46' N, 58° 30' E) Rd. then 21 km WNW on dirt Rd., Ashgabat Region (CAS 179758-179767); (population 7) Ashgabat (37° 57' N, 58° 23' E), Ashgabat Region (MVZ 216087-216092); (population 8) near Iolotan' [Yolotan] (37° 18' N, 62° 21' E), Mary Region (MVZ 216013).

Data Analysis. - Nei's (1978) unbiased genetic distance and Rogers (1972) genetic similarity were calculated using BIOSYS-1 (Swofford and Selander, 1981). Phenetic clustering was constructed using the neighbor-joining algorithm (Saitou and Nei, 1987), which does not require rate uniformity, using PAUP* 4.0 (Swofford, 1999) and Nei's (1978) unbiased genetic distance.

Results

Variable Loci. - Fifteen of the 31 loci screened show variation among the sampled populations (Table 2). Up to five different allelic states are recognized per loci among populations with no more than four allelic states being present within a population.

Genetic Distances. - Allozymic variation among sampled populations of *Trapelus* is surprisingly low (Table 3). The two geographically most distant samples, the European side of the Caspian-Aral Basin (West Caspian) and Kazakhstan (Almaty), have a Nei's (1978) unbiased genetic distance of only 0.117 across 2500 km. The highest Nei's (1978) unbiased genetic distances recov-

Table 2. Electromorph frequencies for the 15 polymorphic loci from eight populations of *Trapelus* sampled. Localities are West Caspian (WCA), Almaty (ALM), Uzbekistan (UZB), Nephtezavodsk (NEP), Repetek (REP), 70 km NW Ashgabat (NWA), Ashgabat (ASH), Iolotan' (IOL). See text for complete localities of all populations used.

Locus	Electromorph	1-WCA	2-ALM	3-UZB	4-NEP	5-REP	6-NWA	7-ASH	8-IOL
AK	a	0.125							
	b	0.875	0.063	0.167	0.938	0.909	1.000	0.929	1.000
	c		0.938	0.667	0.063	0.091		0.071	
	d			0.167					
EST-D-2	a	1.000	0.313	1.000	1.000	1.000	0.950	1.000	1.000
	b		0.688				0.050		
CK	a	1.000	1.000	1.000	1.000	0.909	1.000	1.000	1.000
	b					0.091			
FBA-1	a								0.500
	b				0.063				
	c		0.125		0.188				
	d	1.000	0.875	1.000	0.750	1.000	1.000	0.929	0.500
	e							0.071	
FBA-2	a	1.000							
	b			1.000	0.875	0.818	0.600	0.929	1.000
	c		1.000		0.125	0.182	0.400	0.071	
GPI-2	a	0.313				0.045	0.150		
	b	0.688	1.000	1.000	1.000	0.864	0.850	1.000	1.000
	c					0.091			
HADH	a	1.000	1.000	0.667	1.000	1.000	1.000	0.929	1.000
	b							0.071	
	c			0.333					
IDDH	a					0.182	0.050	0.071	
	b	1.000	1.000	1.000	1.000	0.818	0.950	0.929	1.000
IDH-1	a	1.000	1.000	0.833	1.000	1.000	1.000	1.000	1.000
	b			0.167					
LDH-2	a				0.375	0.091			
	b	1.000	1.000	1.000	0.625	0.909	1.000	1.000	1.000
MPI	a	0.063						0.071	
	b	0.938	1.000	1.000	1.000	0.955	1.000	0.929	1.000
	c					0.045			
PEP-1	a					0.045	0.100		0.500
	b	1.000	1.000	0.500	1.000	0.727	0.800	0.857	0.500
	c			0.500		0.227	0.100	0.143	
PGM	a				0.063	0.091			
	b	0.125			0.125		0.150		
	c	0.875	1.000	1.000	0.813	0.909	0.850	1.000	1.000
PGDH	a					0.091			
	b		1.000		0.063	0.091			
	c			0.333	0.125	0.045			
	d	1.000		0.667	0.813	0.773	1.000	1.000	1.000
PNP	a	1.000	1.000	1.000	1.000	1.000	0.950	1.000	0.500
	b						0.050		0.500

Table 3. Matrix of genetic distance and identity coefficients from the eight populations of *Trapelus* sampled. Nei's unbiased genetic distance (Nei, 1978) is above the diagonal, Rogers genetic similarity (Rogers, 1972) is below the diagonal and sample sizes are on the diagonal. See text for specimen deposition and complete localities of all populations used.

	1-WCA	2-ALM	3-UZB	4-NEP	5-REP	6-NWA	7-ASH	8-IOL
1. West Caspian (WCA)	**8**	0.117	0.066	0.039	0.034	0.026	0.035	0.064
2. Almaty (ALM)	0.865	**8**	0.088	0.102	0.094	0.094	0.108	0.145
3. Uzbekistan (UZB)	0.886	0.873	**3**	0.031	0.019	0.032	0.021	0.048
4. Nephtezavodsk (NEP)	0.927	0.872	0.910	**8**	0.006	0.009	0.006	0.029
5. Repetek (REP)	0.928	0.865	0.920	0.952	**11**	0.002	0.001	0.026
6. 70 km NW Ashgabat (NWA)	0.949	0.875	0.909	0.947	0.958	**10**	0.003	0.026
7. Ashgabat (ASH)	0.939	0.873	0.931	0.957	0.963	0.964	**7**	0.022
8. Iolotan' (IOL)	0.899	0.836	0.900	0.925	0.920	0.932	0.943	**1**

Genetic Distances among USSR Populations of *Trapelus agilis* Complex

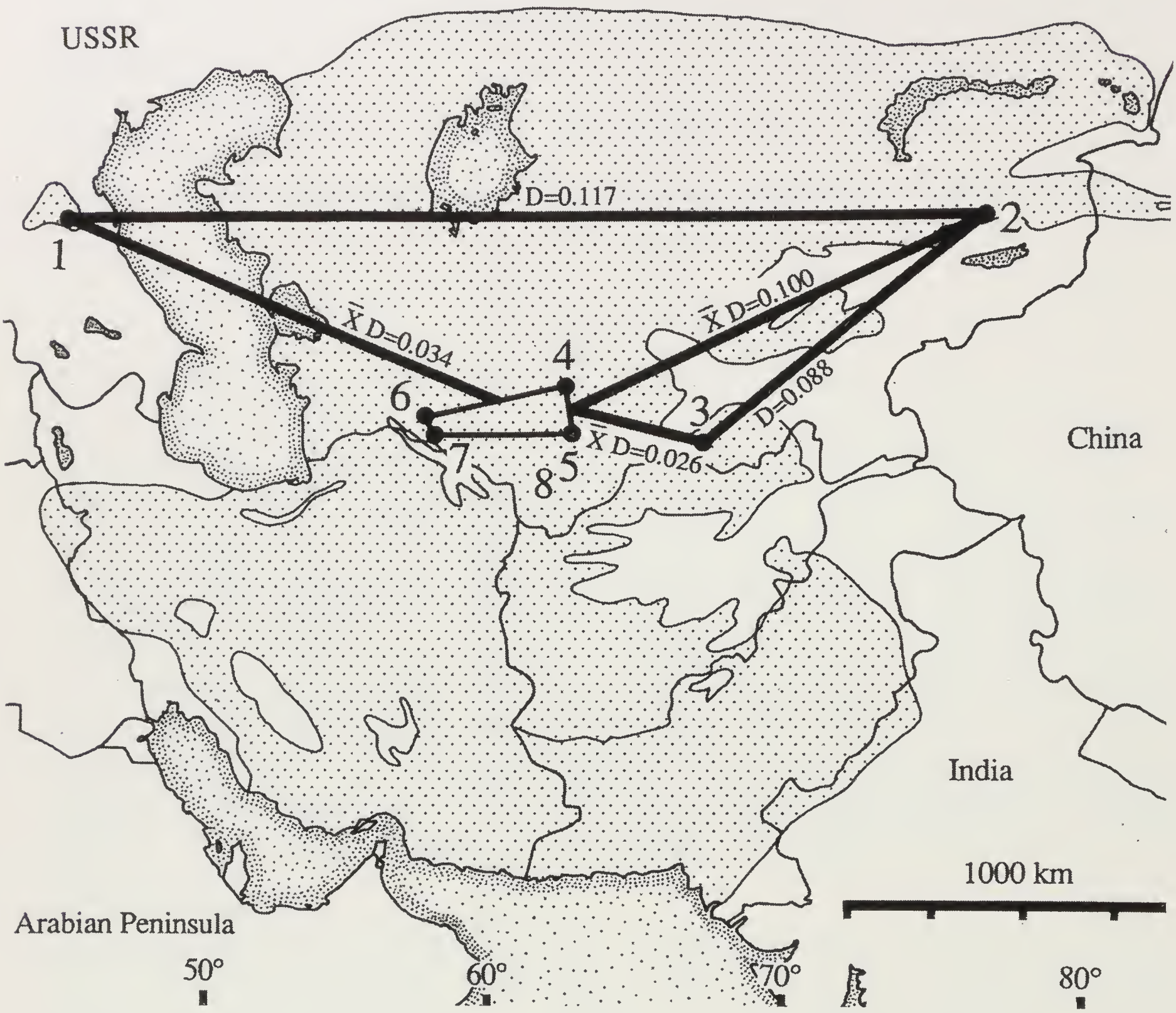

Figure 2. Map of the Caspian-Aral Basin and southwest Asia showing the distribution of the *Trapelus agilis* complex. Dots depict populations sampled. Lines connect populations in major areas, West Caspian, Kazakhstan, Uzbekistan and Turkmenistan. Nei's unbiased genetic distance (Nei 1978) is plotted between areas. The Turkmen populations are averaged. The western most sample on the west side of the Caspian Sea is population 1 (table 3). The eastern most sample is Almaty in Kazakhstan (population 2). To the southwest of this sample is the Uzbekistan population (population 3). Four of the Turkmen samples are connected by lines. The most northeastern is population 4 from Nephtezavodsk and the most southeastern is population 5 from Repetek. The most northwestern is population 6 from 70 km NW Ashgabat and the most southwestern is population 7 from Ashgabat. Population 8 from Iolotan' is not included in the average of Turkmen populations because of the low sample size of one and it is distributed between populations 5 and 7.

ered are 0.088-0.145 (note that the highest value is with a sample size of one) between the northwestern population in Kazakhstan (Almaty) and all other populations sampled in the Caspian-Aral Basin. The European population on the western side of the Caspian Sea is separated from all other populations except the Kazakhstan (Almaty) population by Nei's (1978) unbiased genetic distances of 0.026-0.066. The population in Uzbekistan is distinct from those in Turkmenistan by Nei's (1978) unbiased genetic distances of 0.019-0.048.

Mapping these genetic distances on geography reveals a pattern of isolation by distance in which all distances appear relatively additive (Fig. 2). Clustering of these data in a neighbor-joining phenogram and rooting the tree on the longest path places the Kazakhstan (Almaty) population and Uzbekistan sample in a basal

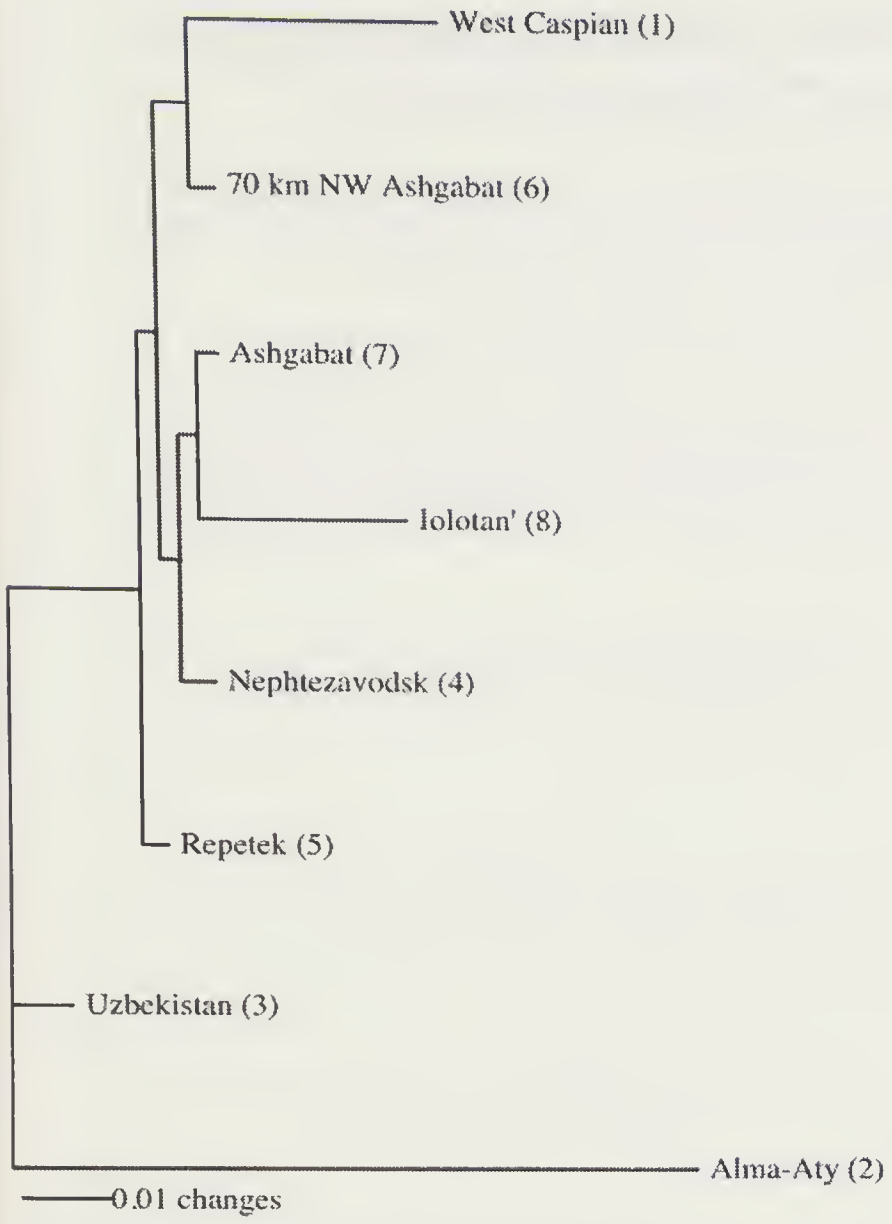

Figure 3. Neighbor-joining phenogram rooted on the longest path. Note that the European population on the western side of the Caspian Sea is nested inside the Asian populations sampled and appears as the sister population to its nearest Asian population (70 km NW Ashgabat). Population numbers corresponding to figure 1, and tables 2 and 3 are given adjacent to locality names.

position. The European (West Caspian) population appears nested within the Turkmen populations and as the sister population to its nearest Asian population (70 km NW Ashgabat), (Fig. 3). This pattern is consistent with the observed genetic distances.

Discussion

The Age of *Trapelus* in the Caspian-Aral Basin. - The European population of *Trapelus* is found to cluster phenetically within the Asian populations with little genetic differentiation, suggesting that these taxa do not represent distinct forms. The low genetic diversity in *Trapelus* of the Caspian-Aral Basin probably indicates a recent dispersion of *Trapelus* throughout the Caspian-Aral Basin. Nei's (1978) unbiased genetic distances do not exceed 0.117 (with the exception of Kazakhstan to Iolotan' Turkmenistan with a sample size of one). A very approximate estimate of divergence time and genetic distance is 14 million years for a Nei's D of 1.0 (Maxson and Maxson, 1979). Given this rate these data suggest a divergence of *Trapelus* populations in the Caspian-Aral Basin at around 1.6 MYBP. This result suggests that *Trapelus* did not diverge in the Caspian-Aral Basin until the Pleistocene, well after the last drying of the Paratethys Sea 3.5 MYBP (Steininger and Rogl, 1984).

Comparison to Other Taxa. - One additional genus of lizard has been sampled from the Caspian-Aral Basin for allozyme variation. The northern populations of the gekkonid genus *Mediodactylus* from Almaty and the Junggar Depression of China show a minimum of two fixed differences when compared to a southern population in the Kara Kum Desert (Macey et al., 2000a). This divergence is greater than those observed among *Trapelus* where no fixed differences are detected between Almaty (population 2) and the Kara Kum Desert (populations 4-8). Because the Caspian-Aral Basin has had periods of inundation followed by drying over the last 6 million years, and the surrounding mountains of the Pamir-Tien Shan are older providing a land refuge (10 million years old; Abdrakhmatov et al., 1996), taxa in the Caspian-Aral Basin may show different levels of divergence.

Taxonomic Recommendations. - Because *Trapelus sanguinolentus* in the Caspian-Aral Basin is distinguished from *Trapelus agilis* of the Iranian Plateau by 10.9% sequence divergence for the mitochondrial DNA segment spanning from *nad1* to *cox1* (Macey et al., 2000b), we consider them separate species. No more than a single fixed difference is observed between populations of *Trapelus* in the Caspian-Aral Basin. Therefore, we interpret these populations to be a single taxon, *T. sanguinolentus*. Further work comparing populations in Southwest Asia is needed in order to determine the specific status of these populations.

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The Feeding Biology of *Rana macrocnemis* Boulenger, 1885 (Anura: Ranidae), Collected in Uludağ, Bursa, Turkey

İSMAIL H. UĞURTAŞ, HIKMET S. YILDIRIMHAN, AND MEHMET KALKAN

Uludağ University Science-Art Faculty, Department of Biology Bursa-Turkey

Abstract. - In this study gut contents of 64 mature specimens (34 male, 30 female) from *Rana macrocnemis* population collected from Uludağ(Bursa) are analyzed. The results indicate that the majority (68.05%) of the food items is composed of insects.

Key words. - *Rana macrocnemis*, feeding, stomach content.

Introduction

Rana macrocnemis is a very common species in the northern and eastern Caucasus and has dispersed into Western and Northern Anatolia in Turkey. Also known as a "mountain frog", its altitudinal distribution ranges from 1,000 to 2,300 m. It generally lives in open areas or in small brooks in or near the woods. It is also seen in areas with muddy bottoms or close to water. Many studies have been conducted to find out the feeding biology of amphibia (Böhme 1975; Boulenger, 1897; Schreiber, 1912; Beschkov, 1970; Lamb, 1984; Yılmaz, 1984; Sampetro, 1986; Gittins, 1987; Atatür, 1993; Uğurtas 1995), but no detailed study exists on the feeding biology of *Rana macrocnemis*. The aim of this study is to establish various animal groups that are taken as prey by this species.

Materials and Methods

The specimens of *Rana macrocnemis* used in this study were collected in three localities between June and July 1997 (Fig. 1). These localities are:
Kirazlyayla (16 males, 30 females)
Hotels Area (10 males)
Çobankaya (8 females)

The specimens were found between the hours 730 and 1930 hours in daylight, but were observed to appear more often between 1030 and 1500 hours. We used Parker (1982), Lodos (1983, 1986), and Çağlar and Demirsoy (1992, 1999) to identify prey items.

Results

We did not observe any significant discrepancies in the stomach contents of males and females. Thus, they were evaluated together. Of the 64 specimens collected during the feeding period, two had empty stomachs. Among stomach contents which were investigated, 626 prey items were counted. Of these prey items, 426 (68.05%) belonged to Insecta, 36 (5.75%) to Arachnida, 44 (7.02%) to Gastropoda, 4 (0.63%) to Myriapoda, 112 (17.89%) to Isopoda and 2 (0.31%) to Acarina groups. Two (0.31%) juveniles of *Rana macrocnemis* were also found as stomach content.

Figure 1. Localities where *Rana macrocnemis* specimens were collected.

The number of prey items found in stomachs and their taxonomy are listed below. It was found that the majority of food taken by *Rana macrocnemis* was composed of insects (68.05%). 144 (36.15%) were Coleoptera, 82 (19.24%) Plecoptera, 94 (22.06%) Diptera, 40 (9.38%) Hymenoptera, 36 (8.45%) Odonata, 6 (1.40%) Orthoptera, 6 (1.40%) Lepidoptera, 4 (0.93%) Homoptera and four (0.93%) in Hemiptera (Fig. 2). As a result of this study on the stomach contents, we con-

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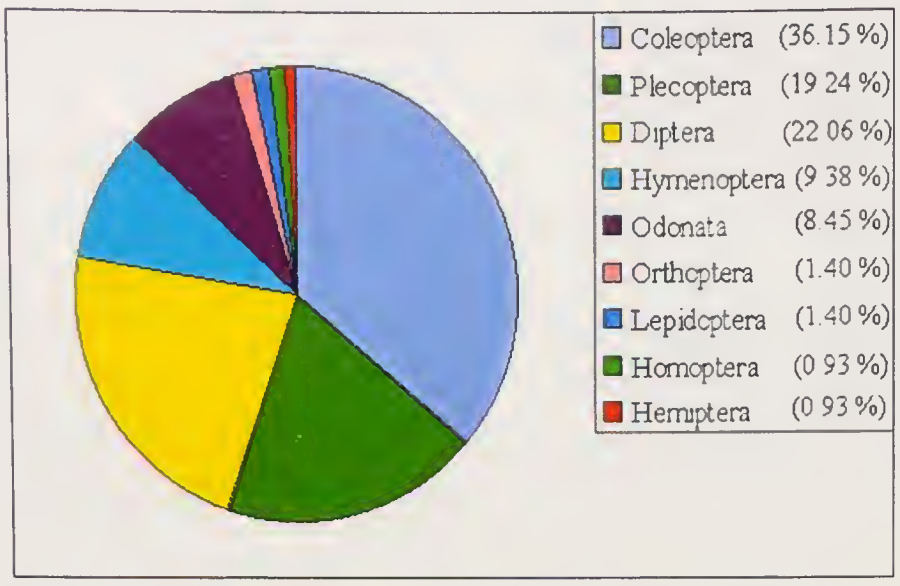

Figure 2. The precentages of insect groups taken as prey.

clude that *Rana macrocnemis* is an opportunitic feeder that utilizes any prey in its environment that it has the ability to consume.

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Morphological Observations on the Erythrocyte and Erythrocyte Size of Some Gecko Species, Turkey

MURAT SEVINÇ*, İSMAIL HAKKI UĞURTAŞ, HIKMET SAMI YILDIRIMHAN

Uludag University, Science and Art Faculty, Department of Biology, Bursa, Turkey
** To whom correspondence should be addressed; E-mail: smurat@uludag.edu.tr*

Abstract. - In this study, erythrocyte size and morphology of the four gecko species [*Asaccus elisae*, *Hemidactylus turcicus*, *Cyrtopodion scaber* and *C. heterocercus mardinensis* (Gekkonidae)] from Turkey were examined. Forty-two specimens were used in this study, of which twelve were *A. elisae,* eight were *H. turcicus*, twelve were *C. scaber,* and ten were *C. h. mardinensis*. Erythrocyte morphology of these examined species was described using Wright's technique. The sizes of erythrocytes and their nuclei were measured using an ocular micrometer at a magnification of 1600x. The results of this study were compared with previous works on the other reptile species. The longest erythrocytes were found in *H. turcicus* and the shortest in *A. elisae*. In terms of the studied species, the nucleus and erythrocyte sizes were found to be correlated (Gekkonidae: $r = 0.39$; $P < 0.001$).

Key words. - Gekkota, Turkey, erythrocyte.

Introduction

Initial studies on the blood of reptiles described the structures, often comparing them with those of the other vertebrates. Literature on the haematology of reptilian blood are based on a few studies where most were concerned with especially European species (Saint Girons, 1970).

Various authors have focused on the different circulating blood cell types of different reptiles (Taylor and Kaplan, 1961; Heady and Rogers, 1963; Hartman and Lessler, 1964; Szarski and Czopek, 1966; Duguy, 1970; Saint Girons, 1970; Mateo et al., 1984; Canfield and Shea, 1988; Cannon et al., 1996; Alleman et al., 1999; Sevinç et al., 2000; Atatür et al., 2001; Sevinc and Uğurtaş, 2001; Uğurtaş et al., 2003). Some authors have studied seasonal (Hutton, 1960; Cline and Waldman, 1962; Haggag et al., 1966) or sexual (Altland and Thompson, 1958) variations in the number of blood cells of different reptile species. In addition, researchers have studied the number of blood cells of different reptiles (Baker and Kline, 1932; Charipper and Davis, 1932; Altland and Thompson, 1958; Hutton, 1961; Hutchinson and Szarski, 1965; Engbretson and Hutchinson, 1976; Mateo et al., 1984). Furthermore, authors have also studied haemoglobin and hematocrit content of blood and hematopoiesis of different reptiles (Altland and Thompson, 1958; Hutton, 1961; Goin and Jackson, 1965; Engbretson and Hutchinson, 1976; Newlin and Ballinger, 1976; Mateo et al., 1984; Alleman et al., 1999).

In Turkey, hematological studies have generally been conducted on humans and some economically important animals. However, there are few hematological studies of the reptiles living in this country (Sevinç et al., 2000; Atatür et al., 2001; Sevinç and Uğurtaş, 2001; Uğurtaşet al., 2003).

In the current study, our aim was to describe and measure erythrocytes of *Asaccus elisae* (Werner, 1895), *Hemidactylus turcicus* (Linnaeus, 1758), *Cyrtopodion scaber* (Heyden, 1827) and *C. heterocercus mardinensis* (Mertens, 1924) which live in Turkey. This study is the first of its kind on Turkish species.

Materials and Methods

In this study, twelve (6 males, 6 females) individuals of *Asaccus elisae,* eight (4 males, 4 females) of *Hemidactylus turcicus,* twelve (8 males, 4 females) of *Cyrtopodion scaber* and ten (4 males, 6 females) of *C. heterocercus mardinensis* (Gekkonidae) were examined. Twenty-two specimens examined were male and twenty were female.

The study was performed on 01-05 June 2000. *H. turcicus* species were collected from Hatay (36° 34' N, 36° 09' E) and the other specimens were from şanlıurfa (36° 53' N, 39° 02' E) (Fig. 1; Table 1). Blood was obtained by cutting the tail (Duguy, 1974). Immediately after blood was obtained in heparinized capillary tubes, blood smears were prepared. Three or five blood smears were prepared per individual. The smears were air-dried and stained with Wright's stain (Hartman and Lessler, 1964). Twelve drops of Wright's stain were dropped on the slides and allowed to remain on the slide one and half minutes before rinsing with phosphate buffer (pH 6.5). The slides were allowed to stand for ten minutes at room temperature, were washed with distilled water, and allowed to dry.

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Figure 1. Collection localities.

On each slide, fifty mature erythrocytes and their nuclei were measured by means of an ocular micrometer at a magnification of 1600x. In this way fifty erythrocyte sizes were calculated. Erythrocyte and nucleus measurements of examined species are given in tables 2-5. Erythrocyte and nucleus sizes were, respectively, calculated according to the formulas [(EL x EW x pi) / 4] and [(NL x NW x pi) / 4]; where EL is the erythrocyte length, EW is the erythrocyte width, NL is the nucleus length and NW is the nucleus width.

Results

Erythrocytes, or red blood cells, of geckos are nucleated, oval cells. Their nuclei are also oval and centrally located, like those of the other reptiles. The cytoplasm of mature erythrocytes appeared both light, dark pink, and homogeneous under Wright's stain. Nuclei of mature erythrocytes are chromophilic (Figs. 2-5).

Because there were no significant differences between the erythrocyte sizes of female and male geckos, data from the females and males of individual species were combined.

The longest erythrocytes were found in *Hemidactylus turcicus*. The mean length of mature erythrocyte of *H. turcicus* was 16.98 mm (± 1.26 standard deviations, with a range of 14.64-19.52 mm) (Table 2; Fig. 6) and also erythrocyte size and length/width ratios of *H. turcicus* are given in table 2.

The shortest erythrocytes were found in *Asaccus elisae*. The mean length of mature erythrocytes of *A. elisae* was 14.96 mm (± 0.79 standard deviations, with a range of 13.42-17.08 mm) (Table 3; Fig. 6). Erythrocyte size and length/width ratios of *A. elisae* are given in table 3.

The widest erythrocytes were found in *Cyrtopodion scaber*. The mean width of mature erythrocytes of *C. scaber* was 10.26 mm (± 0.78 standard deviations, with a range of 8.54-12.20 mm) (Table 4; Fig. 7). Erythrocyte size and length/width ratios of *C. scaber* are given in table 4.

The narrowest erythrocytes were found in *Cyrtopodion heterocercus mardinensis*. The mean width of mature erythrocyte of *C. h. mardinensis* was 9.18 mm (± 0.70 standard deviations, with a range of 6.71-10.98 mm) (Table 5; Fig. 7) and also erythrocyte size and length/width ratios of *C. h. mardinensis* are given in table 5.

The longest nuclei were found in *Cyrtopodion scaber*. The mean length of mature nuclei of *C. scaber*

Table 1. Materials list. NM: number of males; NF: number of females; CD: collection date; CL: collection locality. All specimens are from the Zoology Museum in Uludag UniversityScience and Art Faculty, Department of Biology.

Species	NM	NF	CD	CL
Asaccus elisae	6	6	1-3 June	Sanliurfa
Hemidactylus turcicus	4	4	4-5 June	Hatay
Cyrtopodion scaber	8	4	1-3 June	Sanliurfa
C. heterocercus mardinensis	4	6	1-3 June	Sanliurfa

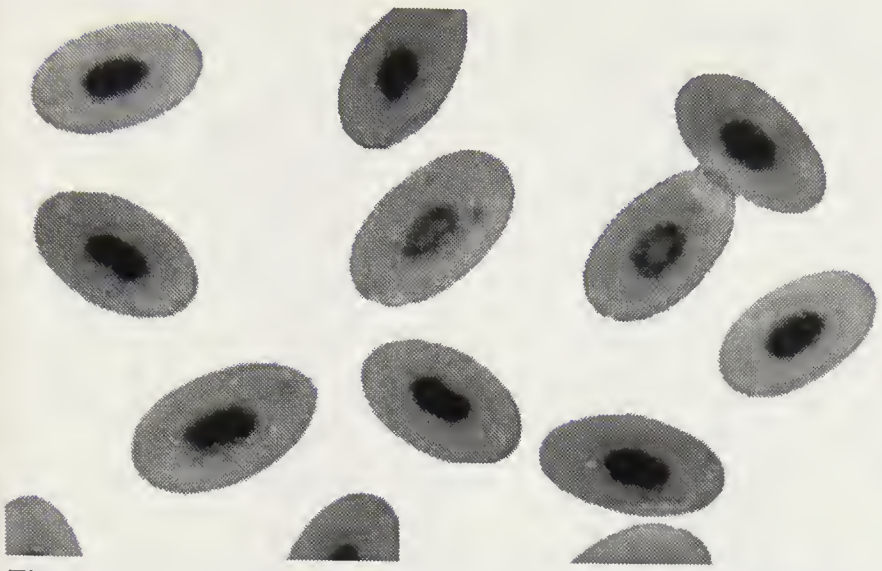

Figure 2. Erythrocyte and nucleus sizes of *Hemidactylus turcicus*.

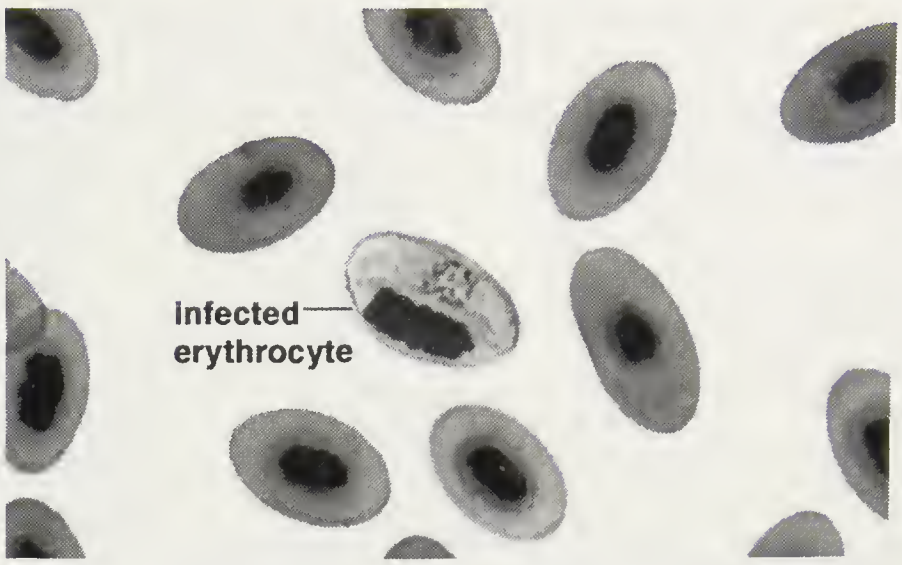

Figure 3. Erythrocyte and nucleus sizes of *Asaccus elisae*.

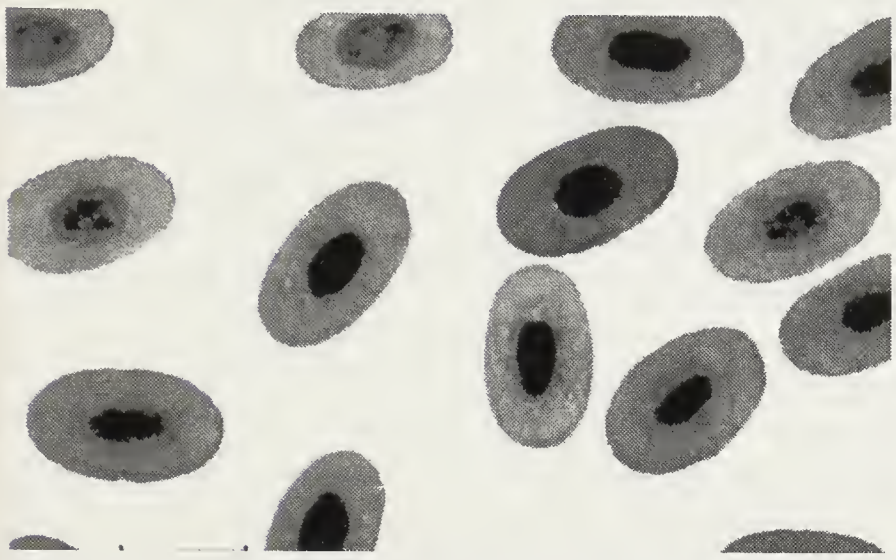

Figure 4. Erythrocyte and nucleus sizes of *Cyrtopodion scaber*.

Figure 5. Erythrocyte and nucleus of *Cyrtopodion heterocercus mardinensis*.

was 6.81 mm (± 0.60 standard deviations, with a range of 5.49-8.54 mm) (Table 4; Fig. 6). Nucleus size and length/width ratios of *C. scaber* are given in table 4.

The shortest nuclei were found in *Asaccus elisae*. The mean length of mature nuclei of *A. elisae* was 6.06 mm (± 0.58 standard deviations, with a range of 4.88-7.32 mm) (Table 3; Fig. 6). Nucleus size and length/width ratios of *A. elisae* are given in table 3.

The widest nuclei were found in *Cyrtopodion heterocercus mardinensis*. The mean width of mature nuclei of *C. h. mardinensis* was 3.78 mm (± 0.44 standard deviations, with a range of 3.05-4.88 mm) (Table 5; Fig. 7). Nucleus size and length/width ratios of *C. h. mardinensis* are given in table 5.

The narrowest nuclei were found in *Hemidactylus turcicus*. The mean width of mature nuclei of *H. turcicus* was 3.53 mm (± 0.42 standard deviations, with a range of 3.05-4.27 mm) (Table 2; Fig. 7). Nucleus size and length/width ratios of *H. turcicus* are given in table 2.

Discussion

Investigations carried out by various authors (Hartman and Lessler, 1964; Szarski and Czopek, 1966; Saint Girons, 1970; Sevinç et al., 2000; Sevinç and Uğurtaş, 2001; Atatür et al., 2001; Uğurtaş et al., 2003) reported that the sizes of erythrocytes vary in members of the four orders of reptiles.

Within the class Reptilia, the largest erythrocytes are seen in *Sphenodon punctatus*, turtles, and crocodilians (Hartman and Lessler, 1964; Saint Girons, 1970; Alleman et al., 1984).

Cryptodiran turtles have the largest erythrocytes from all previously studied reptiles (Saint Girons, 1970). The shortest erythrocytes are found in the Lacertidae family (Hartman and Lessler, 1964; Saint Girons, 1970; Sevinç et al., 2000; Sevinç and Uğurtaş, 2001).

Saint Girons (1970) reported erythrocytes and nuclei measurements of some gecko species. In *Coleonyx variegatus,* erythrocyte length is 18.9 µm and width is 9.6 µm; nucleus length is 7.3 µm and width is 3.7 µm. In *Gehyra variegata,* erythrocyte length is 17.2 µm and width is 11.5 µm; nucleus length is 6.3 µm and width is 3.8 µm. In *Heteronota binoei,* erythrocyte length is 21.4 µm and width is 10.7 µm; nucleus length is 8.1 µm and width is 3.4 µm.

Table 2. Erythrocyte dimensions of *Hemidactylus turcicus* with standard deviations. EL: erythrocyte length; EW: erythrocyte width; ES: erythrocyte size; NL: nucleus length; NW: nucleus width; NS: nucleus size.

	EL (µm)	EW (µm)	EL/EW (µm)	ES (µm)	NS/ES (µm)
Maximum	19.52 ± 1.26	11.59 ± 0.67	2.07 ± 0.14	166.50 ± 15.45	0.20 ± 0.02
Minimum	14.64 ± 1.26	7.93 ± 0.67	1.42 ± 0.14	94.93 ± 15.45	0.09 ± 0.02
Mean	16.98 ± 1.26	9.69 ± 0.67	1.76 ± 0.14	129.50 ± 15.45	0.14 ± 0.02
	NL (µm)	NW (µm)	NL/NW (µm)	NS (µm)	
Maximum	7.93 ± 0.59	4.27 ± 0.42	2.40 ± 0.22	26.58 ± 3.17	
Minimum	4.88 ± 0.59	3.05 ± 0.42	1.43 ± 0.22	11.68± 3.17	
Mean	6.41 ± 0.59	3.53 ± 0.42	1.83 ± 0.22	17.84± 3.17	

Table 3. Erythrocyte dimensions of *Asaccus elisae* with standard deviations. EL: erythrocyte length; EW: erythrocyte width; ES: erythrocyte size; NL: nucleus length; NW: nucleus width; NS: nucleus size.

	EL (µm)	EW (µm)	EL/EW (µm)	ES (µm)	NS/ES (µm)
Maximum	17.08 ± 0.79	10.98 ± 0.66	2.08 ± 0.14	142.00 ± 10.38	0.27 ± 0.03
Minimum	13.42 ± 0.79	7.32 ± 0.66	1.29 ± 0.14	83.54 ± 10.38	0.11 ± 0.03
Mean	14.96 ± 0.79	9.26 ± 0.66	1.62 ± 0.14	108.80 ± 10.38	0.16 ± 0.03
	NL (µm)	NW (µm)	NL/NW (µm)	NS (µm)	
Maximum	7.32 ± 0.58	4.88 ± 0.41	2.40 ± 0.25	23.37 ± 2.47	
Minimum	4.88 ± 0.58	3.05 ± 0.41	1.14 ± 0.25	11.68 ± 2.47	
Mean	6.06 ± 0.58	3.62 ± 0.41	1.69 ± 0.25	17.24 ± 2.47	

Table 4. Erythrocyte dimensions of *Cyrtopodion scaber* with standard deviations. EL: erythrocyte length; EW: erythrocyte width; ES: erythrocyte size; NL: nucleus length; NW: nucleus width; NS: nucleus size.

	EL (µm)	EW (µm)	EL/EW (µm)	ES (µm)	NS/ES (µm)
Maximum	18.30 ± 0.88	12.20 ± 0.78	1.93 ± 0.13	175.30 ± 13.93	0.23 ± 0.02
Minimum	14.64 ± 0.88	8.54 ± 0.78	1.33 ± 0.78	102.20 ± 13.93	0.10 ± 0.02
Mean	16.20 ± 0.88	10.26 ± 0.78	1.59 ± 0.78	130.60 ± 13.93	0.15 ± 0.02
	NL (µm)	NW (µm)	NL/NW (µm)	NS (µm)	
Maximum	8.54 ± 0.60	4.88 ± 0.47	2.75 ± 0.26	30.38 ± 3.42	
Minimum	5.49 ± 0.60	2.44 ± 0.47	1.38 ± 0.26	12.85 ± 3.42	
Mean	6.81 ± 0.60	3.65 ± 0.47	1.89 ± 0.26	19.53 ± 3.42	

Table 5. Erythrocyte dimensions of *Cyrtopodion heterocercus mardinensis* with standard deviations. EL: erythrocyte length; EW: erythrocyte width; ES: erythrocyte size; NL: nucleus length; NW: nucleus width; NS: nucleus size.

	EL (µm)	EW (µm)	EL/EW (µm)	ES (µm)	NS/ES (µm)
Maximum	17.69 ± 0.85	10.98 ± 0.70	2.27 ± 0.16	147.20 ± 11.00	0.28 ± 0.03
Minimum	14.03 ± 0.85	6.71 ± 0.70	1.39 ± 0.16	80.33 ± 11.00	0.12 ± 0.03
Mean	15.65 ± 0.85	9.18 ± 0.70	1.71 ± 0.16	112.80 ± 11.00	0.17 ± 0.03
	NL (µm)	NW (µm)	NL/NW (µm)	NS (µm)	
Maximum	7.93 ± 0.62	4.88 ± 0.44	2.40 ± 0.25	30.38 ± 3.10	
Minimum	5.49 ± 0.62	3.05 ± 0.44	1.13 ± 0.25	13.14 ± 3.10	
Mean	6.56 ± 0.62	3.78 ± 0.44	1.76 ± 0.25	19.49 ± 3.10	

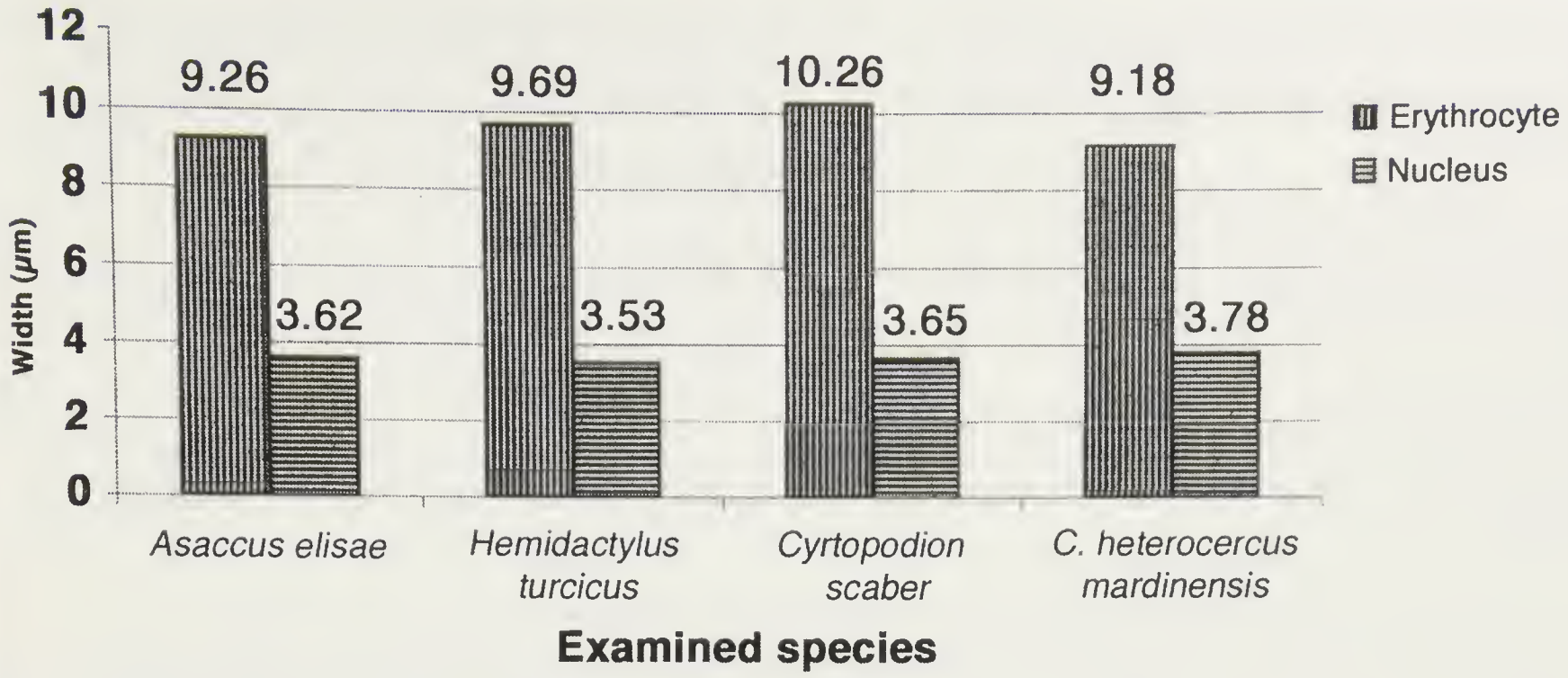

Figure 6. Erythrocyte and nucleus lengths of examined specimens.

Cannon et al. (1996) reported the leukocyte morphology and size of the roughtail gecko *Cyrtopodion scabrum*. However, they did not report any information on the erythrocyte of this species.

In reptiles, the numbers of erythrocytes are smaller than in mammals or birds. Lizards have more erythrocytes than snakes, and turtles have the fewest. Since lizards have the smallest erythrocytes of all reptiles, and turtles the largest, there may be an inverse correlation between the number of erythrocytes and their size; this hypothesis was advanced by Ryerson (1949) (Duguy, 1970).

In this study, the longest erythrocytes were found in *H. turcicus*, the shortest in *A. elisae*, the largest in *C. scaber* and the narrowest in *C. heterocercus mardinensis*. The longest nuclei were found in *C. scaber*, the shortest *A. elisae*, the largest in *C. heterocercus mardinensis* and the narrowest in *H. turcicus* (Tables 2-5; Figs. 6,7).

In the present study, erythrocyte morphology and the results of erythrocytes and nuclei sizes (Tables 2-5; Figs. 6,7) are agreement with the other results carried out by (Saint Girons, 1970).

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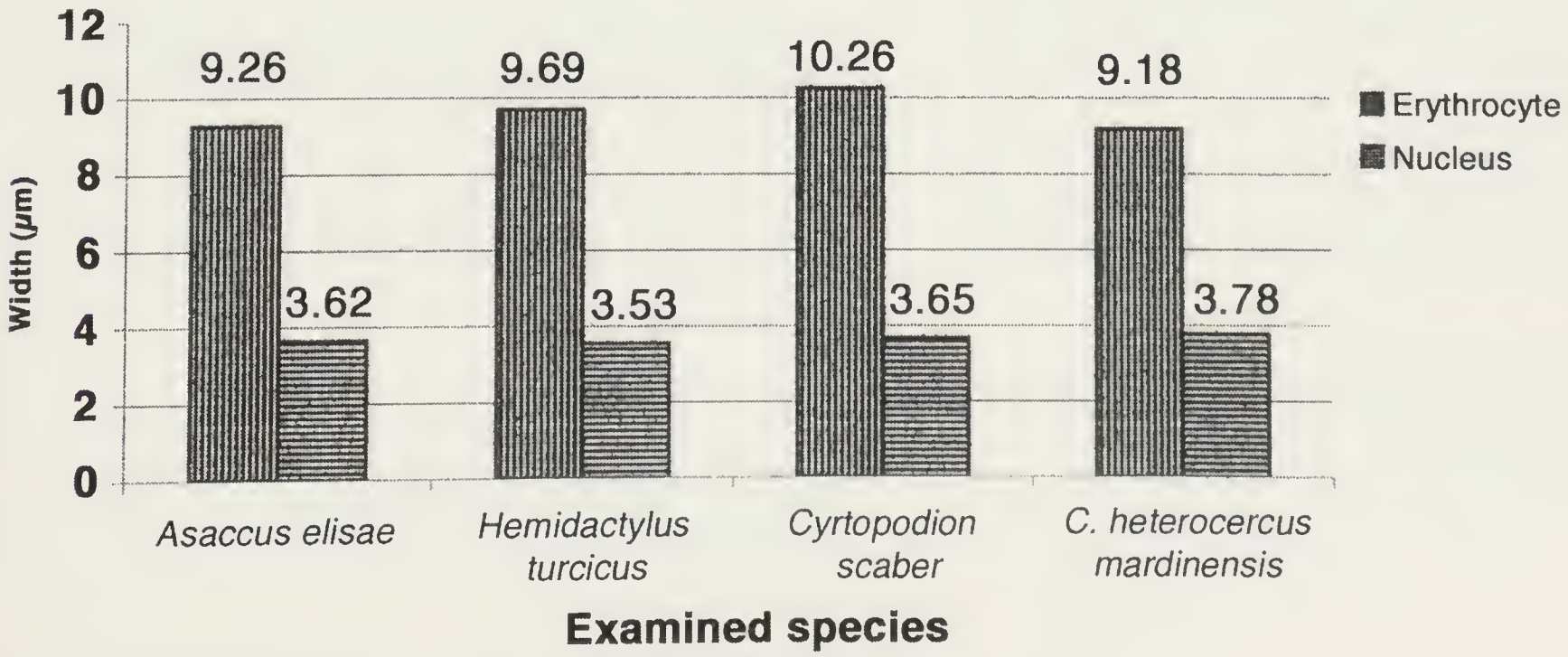

Figure 7. Erythrocyte and nucleus widths of examined species.

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Distribution and Conservation Status of *Neurergus microspilotus* (Caudata: Salamandridae) in Western Iran

MOZAFAR SHARIFI* AND SOMAYEH ASSADIAN

Department of Biology, Faculty of Science, Razi University, Kermanshah, Iran.
**E-mail: sharifimozafar@hotmail.com*

Abstract. - Field and laboratory observations of the Yellow Spotted Newt, *Neurergus microspilotus* (Nestrov, 1917), in western Iran have yielded preliminary data on conservation biology and distribution of this species. New distributional ranges have been determined for *Neurergus microspilotus* in its Iranian range in the mid-Zagros Mountains. In streams occupied by *Neurergus microspilotus,* dissolved oxygen, temperature, discharge, NO_3, and PO_4 were measured. Land use practices, adjacent riparian habitats and channel substrate were also determined. Four new stream habitats were identified. On the basis of interviews with local inhabitants, three other streams were identified as likely habitat for *Neurergus microspilotus*. Measurements of relative abundance of *N. microsphilotus* indicate that this animal is likely to occur in higher numbers in cold and first order streams located at high altitudes in the western edge of the Iranian plateau on the mid-Zagros Range. The limiting factor for the yellow spotted newts in western Iran appears to be human disturbance. In the last four years, one of the five known streams with *N. microspilotus,* in the area of Ghorighala, has virtually lost its entire population due to pollution by a tourist facility and local sewage effluence.

Key words. - *Neurergus microspilotus*, salamander, first order stream, distribution, conservation.

Introduction

Available information on the conservation biology of the western Iranian salamanders is scarce. Investigations made in the 1970s (Schmidtler and Schmidtler, 1975) indicated that three of four species of salamanders belonging to the genus *Neurergus* (*N. crocatus*, *N. microspilotus* and *N. kaiseri*) occur in Iran. There is no recent information on distribution and abundance of these species for assessment of conservation. However, a world-wide concern over declines in amphibian populations (Wake, 1991; Gardner, 2001) is equally pertinent in remote areas of western Iran. Amphibians are sensitive to land-use alteration (Wilkins and Peterson, 2000) and there is widespread concern that environmental pollution and land deterioration are responsible for their decline (Richardson, et al 2000). Several factors are known to have contributed to the declines, including habitat destruction (Sala et al, 2000), fragmentation of habitat (Sjogren, 1991, Marsh and Trenham, 2000), and alteration of species composition of communities through the introduction of exotic predators and pathogens (Beebee, 1977). In addition, acidification and other chemical pollution, alteration of climate (Pounds and Crump, 1994), disease and road kill (Carey, 1993, 2000) are candidates for the amphibian decline.

Relatively few caudate species occur in Iran. These include seven species of the genera *Triturus*, *Batrachuperus*, *Neurergus,* and *Salamandra* (Balutch and Kami, 1995). Newts of the genus *Neurergus* have a relatively wide geographic distribution, ranging from western Iran (Zagros Mountains) and extending into Iraq and southern Turkey (Balutch and Kami, 1995). There is no sufficient information regarding the geographic distribution of the three species of newts that occur in western Iran. Previous investigations indicate that the primary distribution range of *Neurergus microspilotus* is in the mid-Zagros range at the border of Iran and Iraq (Nesterov, 1917; Schmidtler and Schmidtler, 1975). This information also indicates that *Neurergus kaiseri* and *Neurergus crocatus* are expected to occur in southern and northern parts of the Zagros Range, respectively. Recent investigations on *N. microspilotus* confirms that this newt occurs in highland streams in the mid-Zagros region (Assadian and Sharifi, 2002; Rastegar Pouyani and Assadian, 2002).

The aims of the present study are to determine the geographic distribution and conservation biology of *Neurergus microspilotus*. To improve conservation efforts related to this species, information is needed on physico-chemical characters of the habitat. For this reason, we measured some variables in the aquatic environment and adjacent terrestrial habitats.

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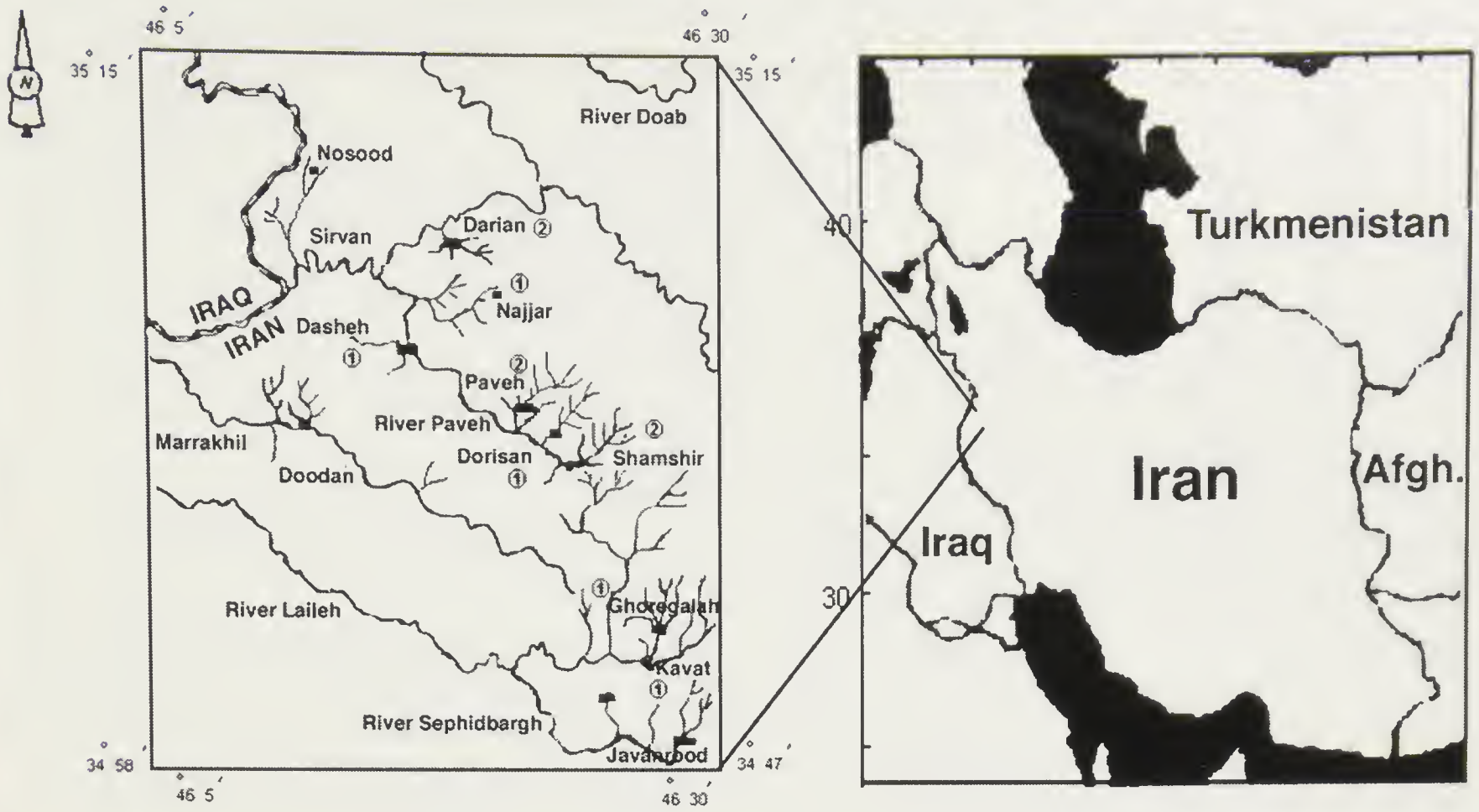


Figure 1. Geographic distribution of *Neurergus microspilotus* in streams of the mid-Zagros Range in western Iran. Those streams with the species have been shown by **(1)**. Those streams that expected to have the animal are shown by **(2)**.

Study Areas

The Iranian basin is a large triangular depression flanked by Elbourz Mountains in the north and the Zagros Mountains in the west. The Zagros Mountains extend diagonally from eastern Turkey to the north of the Persian Gulf and Pakistan border. This range is part of a greater geographic unit arising from the east of the Anatolian Plateau of Turkey and expanding southward to include Iran, Afghanistan, Pakistan and further east to the western edge of the Tibetan Plateau. The Zagros Mountains act as barriers to the incoming air parcels from the west and receive precipitation according to their height and longitude. In general, the northern and western portions of the range receive considerably more rainfall than those in the south and east. The average annual precipitation in the northern Zagros ranges from 400 to 800 mm. per year. Most of the central and southern Zagros receive between 300 and 500 mm (Ghobadian, 1990).

The western Zagros Range meets the northern Mesopotamian Plain, a low land with a hot and dry climate. In some parts of the Zagros Range, where this meeting takes place over a relatively short distance a steep environmental gradient is encountered where high altitude and cold climate from the Iranian Plateau diffuse into the low altitude and warm Mesopotamian Plain in just few kilometers. The weather condition in the western edge of the Iranian Plateau in the mid-Zagros Range is characterized by a pronounced seasonal variation including a long freezing period in winter and a mild summer. Although the average annual precipitation in this area is around 500 mm, most of this comes as snow. As a result, many seasonal and permanent streams at the western side of the Zagros Range are nourished by heavy snow accumulated on the high mountains. In the lowlands of the northern Mesopotamian Plain, which in some parts lie only 20 or 30 km from cold uplands, summers are hot and dry and winters are free of frost. Precipitation in this area approaches 400 mm per annum, rarely appearing as snow. Information obtained from Ravansar Synoptic Station (20 km from Kavat Stream in the highlands) and Sarepolezahab on the northern Mesopotamian Plain (40 km away from Kavat Stream) summarizes the annual climatological data for these two contrasting environments.

Materials and Methods

Streams, ponds, and springs were searched for adults and larvae of *Neurergus microspilotus* in the mid-Zagros Range in Kermanshah and Kurdistan provinces in western Iran in the spring and summer 2001 and 2002. In streams where the salamander was found, channel substrate, channel width, adjacent riparian plant community type, and land use practice were determined. Where possible, relative abundance of *N. microspilotus* was deter-

Table 1. Altitude at head stream, approximate length of the streams and amount of discharge (l/s) in streams where *Neurergus microspilotus* was sighted.

Stream	Altitude (m)	Approximate Length (km)	Position (l/s)	Discharge
Kavat	1500	4	34° 53' N, 46° 31' E	625.7*
Dorisan	1600	3	35° 21' N, 46° 24' E	35**
Dareh Najar	1400	2	35° 06' N, 46° 19' E	-
Ghorighaleh	1600	0.1	34° 54' N, 46° 30' E	333.7*
Paveh rood	1100	2.3	35° 06' N, 46° 17' E	-
Darian	1000	2	35° 08' N, 46° 19' E	-
Shamshir	1800	1.5	34° 59' N, 46° 25' E	-
Marakhil	1600	2.5	35° 02' N, 46° 11' E	-

* Based on measurement made by department of water resource.
** - Discharge measured in field by determining the velocity of water and the extent of cross-section.

mined and expressed as individuals per every ten paces. In small streams where there was no routine hydrological measurement of water discharge, the water discharge was estimated by measuring velocity of water and extent of cross-section width of the channel. In Kavat Stream, where highest relative abundance of *N. microspilotus* was found, visual estimates were made of percent channel substrate composition (Wilkins and Peterson, 2000) by bedrock, boulder (>256mm diameter), cobble (64-256 mm diameter), gravel (16-64 mm diameter), pebble (2-16 mm diameter), fine sediment and coarse woody debris. In these streams several water characteristics were measured. These include dissolved oxygen (Winkler method), temperature (glass thermometer), electrical conductivity (conductivity meter), NO_3 and PO_4 (spectrophotometer).

Results

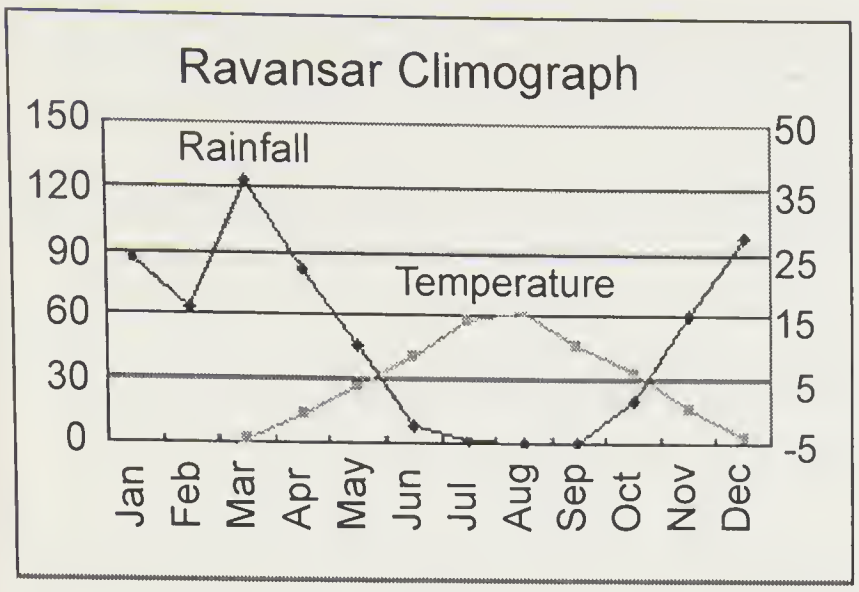
The geographic distribution of *Neurergus microspilotus* in its Iranian range is shown in Figure.1. These are Kavat Stream (34° 53′ N, 46° 31′ E), Dorisan Stream (35° 21′ N, 46° 24′ E), Ghorighaleh Stream (34° 54′ N, 46° 30′ E), Najar Stream (35° 06′ N, 46° 19′ E), and Paveh Rood Stream (35° 06′ N, 46° 17′ E). Apart from streams in which the newt has already been observed, there are three other streams where, on the basis of interviews with local inhabitants, the presence of this animal is likely. These streams are upstream of Marakhil River (35° 02' N, 46° 11' E), Shamshir Stream (34° 59' N, 46° 25' E) and Hajij Stream (35° 08' N, 46° 19' E). Altitude, approximate length of the streams in which *N. microspilotus* is expected to occur, geographic position, and water discharge are shown in Table 1.

Physico-chemical characteristics in streams with *N. microspilotus* are shown in Table 1. Water analysis has been carried out in upper and lower reaches of Ghorighala Stream in order to demonstrate the human impact on the water quality.

Occurrence of the yellow spotted newt in different aquatic microhabitats has been evaluated using the Wilkins and Peterson (2000) classification of channel substrate including bedrock, boulder, cobble, gravel, pebble and fine sand sediment. The yellow spotted newt occupies an assortment of aquatic microhabitats during the breeding season. Visual determination of substrate texture in Kavat Stream indicated that this newt tended to occupy substrates that are gravel or pebble (60%). Figure 3 demonstrate the frequency distribution of substrate classes used by this newt.

Table 2. Physico-chemical characteristics of water where *Neurergus microspilotus* was found.

Streams	DO	NO_3-N (mg/l)	PO_4-P (mg/l)	EC (micm /cm)	Temperature (°C)
Head stream in Ghorighala	8.15	0.38	N.D	323	11
Lower reach of Ghorigala	6.65	0.35	N.D	356	11
Dareh nagar	7.8	1.14	N.D	549	15
Kavat	-	-	-	-	11.5
Dorissan	-	-	-	-	11



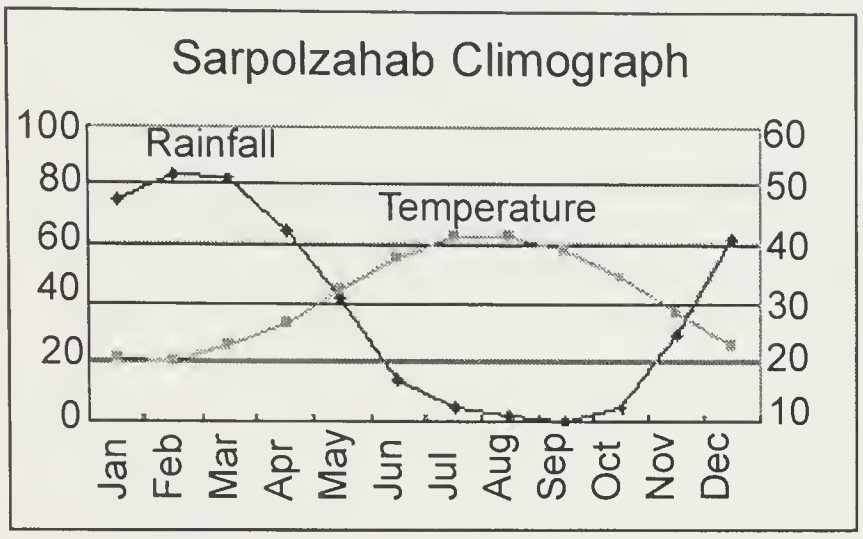


Figure 2. Climographs representing the pattern of precipitation and temperature in Ravansar at the western edge of the Iranian Plateau and Sarepolezahab in the northern Mesopotamian Plain. Data are 20 years mean monthly temperature and rainfall collected at the synoptic stations in these two cities.

Discussion

The presence of *Neurergus microspilotus* in Ghorighaleh Stream has also been reported in previous studies (Nesterov, 1917; Schmidtler and Schmidtler, 1975). Assadian and Sharifi (2002) and Rastegar Pouyani and Assadian (2002) have reported *Neurergus microspilotus* in this stream. Papenfuss and Sharifi also collected several salamanders from this stream in Spring 2000. No information is available regarding the occurrence of *Neurergus microspilotus* in other streams, therefore, the other four streams are new records for *N. microspilotus* in its Iranian range.

All *Neurergus* streams reported in this study with originated from the western edge of the Iranian Plateau (Figure 2) and join to the Dez-Karkheh watershed system in the northern Mesopotamian Plain and finally enter into the Persian Gulf. All these stream are first order streams located at relatively high altitude (1100-1600 m) and join to the main rivers in the lowland (300-600 m) of the catchments (Table 1).

Neurergus microspilotus is a medium size salamander with a slender body. Adults reach a length (snout to vent) of 60-70 mm (mean=65.6, sd=4.63, n=20). Adults are black dorsally and laterally, with greenish yellow blotches. The spots are distributed on the salamander's body without an obvious pattern. *Neurergus microspilotus* characteristically possess broad heads with blunt, rounded snout. *N. microspilotus* is also structured for swimming using their laterally compressed tails for propulsion and steering during swimming.

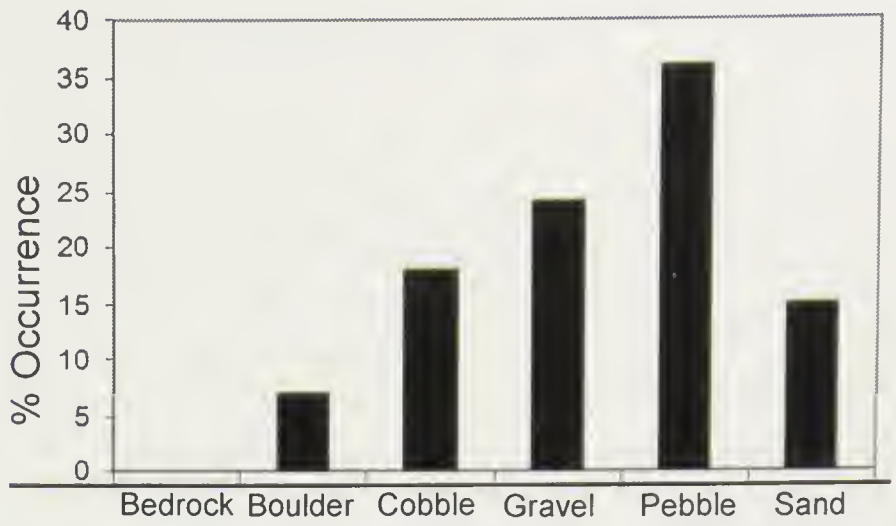


Figure 3. Percent occurrence of *Neurergus microspilotus* in various substrate size group in Kavat Stream (n=42).

The prevailing climatic conditions are distinctly different between and within streams. Since these streams are located at the western edge of the Iranian Plateau, the climatic conditions may vary considerably at the upper reaches compared with lower reaches of the same streams. At the same time it appears that streams closer to the Mesopotamian Plain are experiencing climatic conditions that are different with those that are located at the western edge of the Iranian Plateau. Because of the steep environmental gradient the streams occupied by *Neurergus microspilotus* can be conveniently divided into two groups. Those located in the high altitude and cold weather regions on the western Iranian Plateau (Kavat, Ghorighaleh, Dorisan and Shamshir streams) and those in the north and north eastern part of the range which because of lower elevation experience warmer climate (Marakhil River, Dareh Najar and Darian streams). In Dareh Najar Stream where very few *Neurergus microspilotus* were located, and also in Marakhil and Darian streams where the animal is reportedly seen, it is possible that the animal drifted by the action of water currents. It is also possible that the lower relative abundance in *N. microspilotus* in Dareh Najar and possibly in the other two streams is due to the lower altitude and the vicinity to the northern Mesopotamian Plain.

Terrestrial habitats occupied by *N. microspilotus* include diverse community types including oak-pistachio open woodlands dominated by *Quersus branti* and *Pistachio* spp. This woodland grows on various soil

types, including deep sandy loam soils at the bottom of valleys or gravelly soils on the slopes of steep valleys. In warmer parts of its range, riparian vegetation may also contain willow (*Salix* spp.) or shrubs such as *Cerrasus* and Amygdale (*Amygdalus* spp.). In colder parts of the range the riparian vegetation may be characterized by more hydrophobic plants such as sedges (*Carex* spp.) and sphagnum moss (*Sphagnum* spp.).

Neurergus microspilotus moves from its wintering site to the breeding streams as soon as the spring melt occurs, from late January through early March. Within its range, in high altitude-cold weather regions, egg-laying was observed in early May. However, it appears that the reproductive pattern of *N. microspilotus* is not tightly synchronized because unhatched eggs have been observed as late as mid-June. No breeding activity, eggs, or juveniles of *N. microspilotus* have been observed in the low altitude warm climate part of the range. Eggs of *N. microspilotus* are laid singly or in small clumps on vegetation or on rocks. The number of oocytes in a female dissected in laboratory was 108. Laboratory observations of larval growth and development indicate that larvae complete the metamorphosis in the first year. In early autumn they still possess their gills. Larvae with large heads, well developed dorsal fins, and bushy gills have the ability to react suddenly with a whole body reaction to external stimulus.

Although no information is available regarding wintering activity of *Neurergus microspilotus* in its Iranian range, the appearance of the animal in early spring and disappearance in summer implies that this newt requires both upland and wetland habitat that contain suitable aquatic environment during the breeding season and subterranean burrows appropriate for wintering. These normally include an aquatic environment for breeding and a terrestrial habitat where juveniles and adults spend most of their time.

Habitat loss through divergence of streams for irrigation of cultivated lands is probably the single most important factor that threatens *Neurergus microspilotus* in its Iranian range. Traditionally, due to the lack of land in steep valleys in the mid-Zagros Range, extensive attempts have been made to construct a complex of reinforced terraces of land, which is cultivated for walnut and other orchard trees. Water is diverted from its natural channel to irrigate these lands. Although no harm is directed toward *N. microspilotus* in these orchards, the impact of land use alteration especially in dry periods causes many of these creatures to be deprived of a healthy aquatic environment.

Although human settlement in the mid-Zagros area is characteristically less developed compared with other localities in western Iran, *Neurergus microspilotus* is experiencing an environmental impact similar to that found in more urbanized areas in the country. For example, Ghorighaleh Stream originates from a cave that has been developed by a reclamation project for visitors. Since the construction of this unit the stream is suffering from gross pollution caused by thousands of visitors. Changes in water characteristics in the upper and lower reaches of the stream are shown in Table 2. Although in 2000 and 2001 numerous Yellow Spotted Newts were reported (Assadian and Sharifi, 2002; Rastegar Pouyani and Assadian, 2002) no newts were seen in 2002. The absence of *Neurergus microspilotus* is presumably due to the human impacts resulting from an ecotourism center developed in 1999 at the Ghorighaleh Cave where the source of the stream is located. Massive solid waste disposed by thousands of visitors together with raw sewage released to the stream by residents of Ghorighaleh Village can be observed in the upper reaches of this stream although only changes in dissolved oxygen are evident in physico-chemical characteristics measured in this study.

Conclusions

Although *Neurergus microspilotus* has been virtually extirpated from one of five known breeding streams in its Iranian range, it does not appear to be in immediate danger of extinction because one is likely to find this newt occur in other streams in the area. However, the situation for *N. microspilotus* is not promising as the major threatening factors such as habitat destruction and water pollution are operating. Robust populations occur in at least in one of its habitats (Kavat Stream). However, the lack of information essential to estimate population size and population trends makes it difficult to assess conservation status of this salamander. Future work should examine the long-term effects of anthropomorphic impacts associated with land use alteration and pollution.

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An Investigation on the Blood Cells of the Leopard Gecko, *Eublepharis angramainyu* (Reptilia: Sauria: Eublepharidae)

MURAT TOSUNOĞLU[1], DINÇER AYAZ[2], CEMAL VAROL TOK[1], AND BAŞARAN DÜLGER[1]

[1]*Çanakkale Onsekiz Mart University, Faculty of Science-Literature, Department of Biology, Terzioğlu Campus, Çanakkale, Turkey*

[2]*Ege University, Faculty of Science, Department of Biology, 35100 Bornova, İzmir ,Turkey*

Abstract. - In this study, blood cell counts and sizes in three adult *Eublepharis angramainyu* specimens (one male, two female) collected from SE Anatolia (Sanlurfa – Birecik). The number of erythrocytes in 1 mm^3 ranged between 870,000 and 950,000 (average 910,000). The mean total length of erythrocytes was calculated as 20.35 µm, the width as 10.59, the size as 169.68 μm^2; the mean nucleus length as 7.50 µm, the width as 4.15 and the size as 24.47 μm^2. Small lymphocytes had a mean diameter of 9.78 µm, big lymphocytes 13.71 µm, monocytes 15.37 µm, neutrophiles 16.56 µm, eosinophiles 17.59 µm, and basophiles 12.87 µm. The mean length of thrombocytes was measured at 8.82 µm, and the width at 5.93 µm.

Key words. - *Eublepharis angramainyu*, Sauria, blood cell count, blood smears, erythrocytes, leucocytes, thrombocytes.

Introduction

Eublepharis angramainyu Anderson and Leviton, 1966, also known as the "leopard gecko", was first found between Masjid Soleyman and Batsvand in the Khuzesdan province of Iran. The species was reported to range in the western foothills of the Zagros Mountains and Mesopotamia in Iraq and Iran, and NE Syria with a vertical distribution of 300 to 1000 meters (Anderson and Leviton, 1966; Leviton et al., 1992; Disi and Böhme, 1996; Anderson, 1999). Studies conducted in recent years (Göçmen et al., 2002) established that the species also inhabited SE Anatolia (Sanlıurfa–Birecik). Although there are a number of studies on the distribution, morphology and ecology of the species (Anderson and Leviton, 1966; Leviton et al., 1992; Disi and Böhme, 1996; Anderson, 1999; Göçmen et al., 2002), a literature review has not revealed any detailed haematological studies.

Most studies on the haematology of different species are related to blood cell counts (Alder and Huber, 1923; Hutchison and Szarski, 1965; Duguy, 1970; Arıkan, 1989) and blood cell sizes (Szarski and Czopek, 1966; Hartman and Lessler, 1964; Atatür et al., 1998, 1999). The number haematological studies related to amphibian and reptile species living in Anatolia has been increasing in recent years (Arkan, 1989; Atatür et al., 1998, 1999, 2001; Sevinç et al., 2000). In this study, the number and sizes of blood cells of *Eublepharis angramainyu* were determined and photographs of their blood cells presented.

Materials and Methods

Three adult specimens (one male, two female) examined in this study were collected near Çiçekalan Village between 2200-2400 hours at an altitude of 400 m during the species breeding season (01 July, 2002). Blood samples were taken within the first three days after the specimens were collected live in the wild and brought to the laboratory.

Blood cell counts were carried out by means of Neubauer hemocytometer. Hayem solution was used to dilute the erythrocytes. Wright-Stained blood smears were made use of in the measurement (erythrocytes, leucocytes and thrombocytes) and computation of blood cells. The necessary blood samples were obtained by cardiac (ventriculus) puncture, via heparinized hematocrit capillaries. Blood cell measurements were taken by means of a MOB-1-15x ocular micrometer. On each blood smear, measurements related to 40 randomly chosen erythrocytes (total erythrocyte length, total erythrocyte width, nucleus length and nucleus width) were made, and the nucleus size was calculated) according to the formula EL.EW./4 and the nucleus size according to the formula NL.NW./4 (Duguy, 1970; Atatür et al., 2001). Moreover, micrometric measurements were made on leucoytes and thrombocytes. Photographs of

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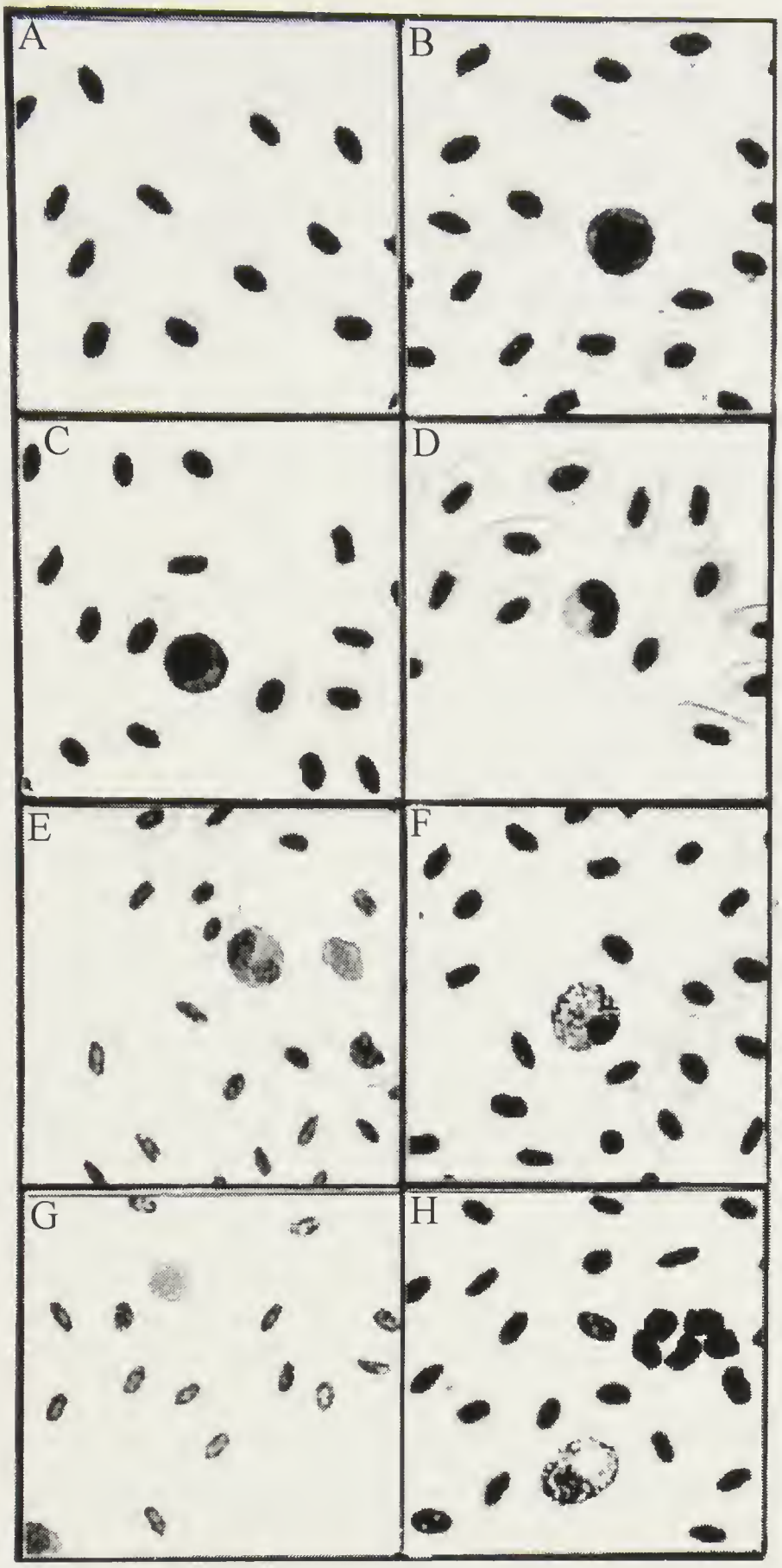

Figure 1: The blood cells of *Eublepharis angramainyu*. A- erythrocytes, B- small lymphocyte, C- large lymphocyte, D- monocyte, E- neutrophil, F- eosinophil, G- basophil, H- a cluster of thrombocytes.

blood cells were taken using a Carl Zeiss Jena microscope at 40x magnification.

Results

Male and female specimens were assessed together as there were no significant differences between them with respect to the number and size of blood cells. As in other lizrds, the erythrocytes belonging to *Eublepharis angramainyu* are also ellipsoidal cells with nuclei. The nuclei are also ellipsoidal, somewhat regular and centrally located (Figure 1A). The mean total length of the erythrocytes (L) was calculated as 20.35 μm the width (W) as 10.59 μm, the size (S) as 169.68 μm^2; the mean nucleus length (NL) as 7.50 μm, the width (NW) as 4.15 μm, and the size (NL) as 24.47 μm^2. The number of erythrocytes in 1 mm^3 of blood ranged between 870,000 and 950,000 (average 910,000) (Table 1).

Lymphocytes have a spherical shape. Both small and large lymphocytes were examined in the blood smears prepared (Figure 1B, C). Large lymphocytes were 13.71 μm in diameter and had a large cytoplasmic zone and a centrally-located, large, round nucleus. The cytoplasm is stained pale blue and the nucleus purplish blue using the Wright Stain. No granule formation was observed in the cytoplasm. Small lymphocytes had a mean diameter of 9.78 μm (Table 1). The large nucleus covers the majority of the cell's area; the cytoplasm is in the shape of a thin ring. Lymphocytes are the most commonly seen leucocytes in the preparates.

Although resembling the large lymphocytes in size, monocytes are easily distinguished from the shape of the nucleus (Figure 1D). They have a mean diameter of 15.37 μm Granule formation was observed in the cytoplasm (Table 1). The nucleus is not oval, but depressed on one side and occupies at least half of the cell. The cytoplasm is stained light purple and the nucleus dark blue. They are the second most common leucocytes after lymphocytes and neutrophiles.

Neutrophiles are spherical cells with a mean diameter of 16.56 μm (Table 1). Using the Wright Stain, the cytoplasm is stained light blue and the nucleus dark blue. There are very fine granules in the cytoplasm (Figure 1E). The nucleus is a structure with lobes and segments. They are the most common leucocytes second to lymphocytes.

Eosinophiles have a diameter of 17.59 μm (Table1). The cytoplasm is stained light blue and the nucleus dark blue. Large, round, bright red granules within the cytoplasm strike eye as the most distinctive characteristic of these cells (Figure 1F). The nucleus was seen to have two lobes. These cells take the fourth place in the preparation of smears after lymphocytes, monocytes and neutrophiles.

Basophiles are oval-shaped with a mean diameter of 12.87 μm (Figure 1G and Table 1). When stained by means of the Wright Stain, dark bluish purple granules within the light blue cytoplasm are in a position marking the dark blue nucleus. These cells are rarely seen in the preparates.

Thrombocytes are spindle-shaped cells with a mean length of 8.82 μm, a width of 5.93 μm (Figure 1H and Table 1). In the Wright-Stained preparates, dark stained cells with large oval nuclei and small irregular cytoplasic zones form groups of two or more.

Table 1: The established counts, measurements and sizes concerning the blood cells of *Eublepharis angramainyu* (in m and m^2). N: Number of specimens; n: Number of measurements/computings in each specimen; Ext: extreme values; SD and SE: standard deviations and the standard errors of the means, respectively.

Blod Cells	N	n	Ext	Mean	SD	SE
Number of Erythrocytes	2	3	870,000-950,000	910,000	-	-
Total Erythrocyte Length	2	40	15.00-22.50	20.35	2.15	0.24
Total Erythrocyte Width	2	40	7.50-12.50	10.59	1.00	0.11
Total Erythrocyte Size	2	40	91.26-220.78	169.68	26.87	3.00
Nucleus Length	2	40	6.25-8.75	7.50	0.41	0.05
Nucleus Width	2	40	3.25-5.25	4.15	0.52	0.06
Nucleus Size	2	40	17.86-31.40	24.47	3.44	0.38
Lymphocyte (big) Diameter	2	20	12.50-16.25	13.71	1.21	0.19
Lymphocyte (small) Diameter	2	20	7.50-11.25	9.78	1.11	0.17
Monocyte Diameter	2	40	11.25-20.00	15.37	2.00	0.31
Neutrophile Diameter	2	40	15.00-20.00	16.56	1.61	0.36
Eosinophile Diameter	2	20	15.00-20.00	17.59	1.56	0.24
Basophile Diameter	2	5	10.00-15.20	12.87	1.81	0.40
Thrombocyte Length	2	40	7.25-11.25	8.82	1.16	0.18
Thrombocyte Width	2	40	5.00-8.25	5.93	0.77	0.12

Table 2: The number of erythrocytes in 1 mm^3 of blood in different lizard species.

Researchers	Species	Number of Erythrocytes
Present study	*Eublepharis angramainyu*	870,000-950,000
Duguy (1970)	*Hemidactylus turcicus*	866,000
	Chalcides ocellatus	806,000
	Agama atra	1,250,000
	Lacerta agilis	945,000-1.420.000
	Lacerta viridis	840,000-1,600,000
	Anguis fragilis	466,000-1,615,000

Table 3: Sizes of erythrocytes and nuclei in different lizard species according to various researchers (EL/EW: Erythrocyte Length/Erythrocyte Width Ratio, ES: Erythrocyte Size (µm²), NL/NW: Nucleus Length/Nucleus Width Ratio, NS: Nucleus Size (µm²), N/C: Nuclear surface/Cell surface ratio).

Researchers	Species	EL/EW	ES	NL/NW	NS	N/C
Present study	*Eublepharis angramainyu*	1.92	169.68	1.80	24.47	0.14
Atatür, et al. (2001)	*Ablepharus chernovi*	1.87	84.12	2.45	12.01	0.14
	Chalcides ocellatus	1.86	91.33	1.98	10.70	0.12
	Mabuya aurata	1.90	84.88	2.01	10.02	0.12
	Ophiomorus punctatissimus	1.96	92.08	2.30	12.70	0.14
	Eumeces schneideri	1.97	92.31	2.81	14.20	0.15
Sevinç, et al. (2000)	*Lacerta rudis*	1.63	87.46	1.64	16.66	0.19
	Lacerta viridis	1.86	125.00	1.94	14.6	0.11
Duguy (1970)	*Eumeces algeriensis*	1.61	154.80	2.10	26.4	0.17
	Anguis fragilis	1.88	143.90	1.62	22.5	0.14

Discussion

As stated in the 'Results' section, *E. angramainyu* specimens were collected during the mating season and did not display sexual dimorphism with respect to the number of erythrocytes and sizes. It has been found that there are significant differences among lizard families with respect to the number and size of erythrocytes, and the members of Gekkonidae have the highest number of erythrocytes among lizards (Alder and Huber, 1923; Hutchison and Szarski, 1965; Duguy, 1970). Values belonging to the number of blood cells determined in diffeent lizard species (Table 2), by various researchers were compared with those we obtained for *E. angramainyu* in the present study, and it was established that the number of erythrocytes in 1 mm^3 of blood was very close to that of *Hemidactylus turcicus* (Gekkonidae) species, but different from that of other lizard species.

Values we obtained in *E. angramainyu* with respect to the sizes of erythrocytes and nuclei were compared with those determined for some lizard species (Table 3), and it was found that values concerning the sizes of erythrocytes and nuclei were very close to those of species belonging to Gekkonidae family. When compared with the other lizard species, *E. angramainyu* can be said to have the largest erythrocytes with respect to the sizes of erythrocytes and nuclei.

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A Record of *Boiga ochracea walli* (Stoliczka, 1870) from Bangladesh

M. Farid Ahsan* and Shayla Parvin

Department of Zoology, University of Chittagong, Chittagong 4331, Bangladesh.
**Corresponding author E-mail: mfahsan@ctgu.edu*

Abstract. - Two specimens of *Boiga ochracea* specimens from Bangladesh are referred to *Boiga ochracea walli*. The locality data for these specimens are lost, but they are probably form the University of Chittagong campus. These are the first records of this subspecies for Bengladesh.

Key words. - *Boiga ochracea*, Bangladesh.

While identifying snake species preserved in the Departmental Museum of Zoology, Chittagong University (CU), two specimens of *Boiga ochracea walli* (Stoliczka, 1870) were found. One was collected in 1975, but the localities where they were found are unknown. Both specimens were probably collected form the University of Chittagong campus. The occurrence of *Boiga ochracea* in Bangladesh was first reported by Khan (1982) based on a specimen collected from Chittagong Hill Tracts. Khan (1982) did not identify the specimen to subspecies. Smith (1943) reported the subspecies range as Burma (now Myanmar) south of Lat. 25°; Tenasserim; the Andaman and Nicobar Islands. Both localities of *Boiga ochracea walli* from Chittagong (this report) and *B. ochracea* from Chittagong Hill Tracts (Khan 1982) are close to Myanmar and south of the latitude mentioned by Smith (1943). This report extends the subspecies range up to Bangladesh and it may occur in other parts of the country like Greater Sylhet, Cox's Bazar, and the districts of Chittagong Hill Tracts (i.e., Rangamati, Khagracheri and Bandarbans) as they have similar habitats.

The CU specimens have the following characters (although the natural colour may have changed due to the effects of preservation): faded greyish above, vertebral series of scales paler than others, ventral side of body whitish. Smith (1943) described the subspecies as "greyish, reddish or yellowish brown above (coral red in life), some of the scales finely edged with black and forming more or less distinct transverse lines or bars, best marked in the young; the vertebral series of scales sometimes lighter than the others; paler below; lips and chin whitish".

The CU specimens have eight supra labials, 4th, 5th and 6th below the eyes; one pre and two post-oculars present. Smith (1943) stated that there is normally one pre-ocular, not reaching the upper surface of the head; anterior genials about as long as the posterior, latter in contact with one another or separated by small scales; vertebrals strongly enlarged. The measurements of the CU specimens are compared below with those reported by Smith (1943).

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Table 1. - The table shows that the Smith's (1943) specimens and the present ones are similar.

Cat. No.	Date locality	Total length (cm)	Tail length (cm)	Dorsal scales	Ventral scales	Anal scale	Caudal scales	Temporal scale	Source
31CU	04.03.75	88	16	19:19:15	236	1	79	2+2	Present work
37CU		50.3	9.3	17:19:15	229	1	97	2+2	
		105-110	23.5-21.5	19:19:15	221-246	1	89-107	2+2 or 2+3	Smith (1943)

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Some Aspects of Breeding Biology of the Bengal Lizard (*Varanus bengalensis*) in Bangladesh

M. Farid Ahsan[1] and M. Abu Saeed[2]

[1]*Department of Zoology, University of Chittagong, Chittagong 4331, Bangladesh; E-mail: mfahsan@ctgu.edu*
[2]*AGROCARE, Golden Plaza (1st Floor), 58 Shaheed Tajuddin Ahmed Sharani, Mohakhali, Dhaka 1212, Bangladesh*

Abstract. - Some aspects of breeding biology of the Bengal, or Gray, Monitor Lizard (*Varanus bengalensis*) were studied in the farm area of Azra Produces Impex (a private enterprise) at Bhaluka, Mymensingh from 1995 to 1997. The feeding success, caring, egg-laying, clutch-size, incubation of neonate care were observed. The eggs were laid between August and October with a mean clutch-size of 21.1 (range 10-32, n=25). The mean incubation period was 192.7 days (range 189-216 days, n=678) with a hatching success of 3.3% which was very low due to many reasons. Some problems regarding farming of the species are discussed.

Key words. - *Varanus bengalensis*, Bengal lizard, breeding, farming, Bangladesh.

Introduction

The Bengal, or Gray, Monitor Lizard (*Varanus bengalensis*) is one of the three varanid species found in Bangladesh. It is most widely distributed throughout the country, including many islands, in both forested and non-forested open wooded areas. It is economically important for its valuable skin and its role in the ecosystem, especially in controlling some pests. In Bangladesh, some tribes like the Shawtal, Kulee, Kukis, etc., also eat its meat.

The few research works that have been done on varanids in Bangladesh mainly deal with their distribution. However, Whitaker and Hikida (1981) and Akond et al. (1982) briefly worked on the ecology and stomach contents of varanids. There is no published report on the captive breeding of varanids of Bangladesh. Azra Produces Impex, a private enterprise, started a project in Bangladesh on the farming of *V. bengalensis*. As advisor (MFA) and consultant (MAS) we looked into the biological aspects of the project. This paper deals with the preliminary observations on feeding, caring, egg-laying, clutch-size, incubation of eggs, and caring of hatchlings. Some problems regarding farming of the species have also been discussed.

Study Area and Study Animals

The *Varanus* breeding farm of Azra Produces Impex is situated at Habirbari of Bhaluka Thana (Mymensign District, Bangladesh, 24° 21' N and 90° 21' E). It is 71 km north of Dhaka City and located adjacent to the Dhaka-Mymensign Highway. The farm was inaugurated in June, 1995 within a concrete boundary wall (about 3 m high including wire rope) enclosure with an entrance (gate) on the western side along the said Highway. The total area of the farm is 37.74 acres (16.77 ha). There are 50 ponds inside the farm and a lake excavated around the periphery of the farm. One open wire-net enclosure (37 m x 61 m x 1 m) with a concrete base (of 25.4 cm) has also been made inside the farm area for some of the lizards (about 200 individuals).

Figure 1. Adult *Varanus bengalensis* eating supplied food.

A total of 2,112 Bengal lizards (685 [32.4%] males and 1427 [67.6%] females) were released inside the farm area. These lizards were captured by professional hunters from wild stock (with the permission of the concerned authority, Ministry of Environment and Forests, Government of the People's Republic of Bangladesh) of Greater Mymensign and Tangail districts between 4 June and 9 September, 1995. Before releasing, each lizard was physically checked and sex recorded. Injured and immature lizards were rejected.

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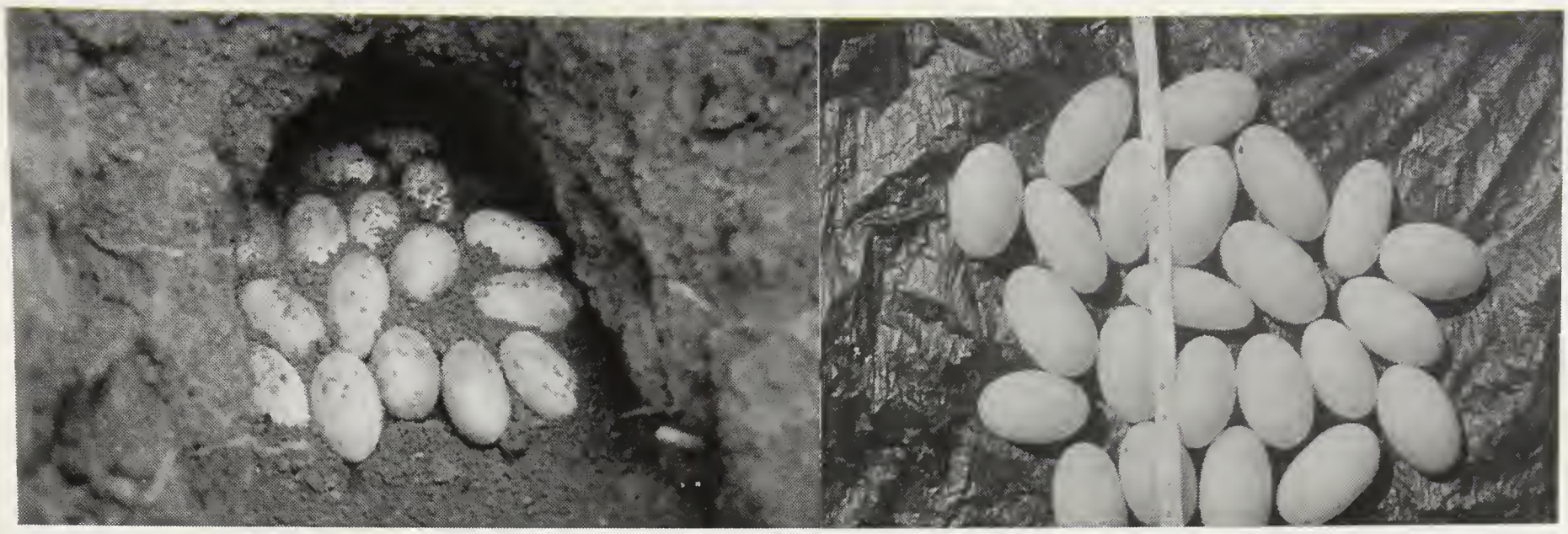

Figure 2. Eggs of *Varanus bengalensis* in a natural nest (left) and being prepared for artificial incubation (right).

Methods

Food. Cleaned pieces of stomach (omasum part only) of bovines, collected from different slaughter houses of Dhaka city, were supplied to the lizards as food. Food was supplied only inside the wire-net enclosure in trays (25.4 cm x 25.4 cm x 5 cm, made up of tin sheet). In other parts of the farm, food was thrown near the roosting places (close to bushes) of the lizards. Usually foods were supplied to the lizards every alternate day (except for Sunday) - half of the farm area was covered in one day and the rest half in the next day. About 100-150 such stomachs were offered to the lizards on every feeding day (Fig. 1).

Eggs. Eggs (Fig. 2, Table 1) were collected from holes in the soil (dug obliquely) and holes of termite mounds (either natural or made by lizards) and placed inside artificial holes made in the incubation cages. Special precautions were taken during handling of eggs to avoid shaking or turing upside down, so that, embryos do not get loose or shift from the original position.

Incubation. An incubation area was selected inside the farm where two cages were built (Fig. 3), each one having a small entrance. Cage-I was closed cart-shaped (12.5 m x 4.6 m x 2.6 m), made of wire-net (mesh size 5 mm x 5 mm) with a concrete base and supported by rods. Inside the cage three artificial incubation beds were built - western (1240 cm x 116 cm x 55 cm), middle (1240 cm x 110 cm x 48 cm) and eastern bed (1240 cm x 95 cm x 32 cm). Spaces between western and middle beds were 53 cm, and between middle and eastern were 43 cm. In each bed, two storied oblique holes were excavated - the western bed had holes only in the eastern side, the eastern only in the western side, and the middle bed had holes on both sides. Sandy, granular, and dry soils were placed on the floor of each hole and dry sands on the hole mouth. The roof of each hole was made by moist sandy loam. The top of each bed was covered with grasses. Each hole (length 30 cm and diameter 10 cm) was marked by numbered stick plate. Altogether there were 190 holes in cage-I and 30 eggs were placed in each hole. When all holes of cage-I were filled with eggs (totalling 5,700), the second cage (cage-II) was built in the eastern periphery of the cage-I. Cage-II was closed rectangular-shaped (12.5 m x 7.9 m x 2.5 m) formed of wire-net (mesh size 5 mm x 5 mm) and supported by rods and poles. Here, only pits were dug, and 30 eggs were placed in each pit. There were 500 such pits (containing 14,499 eggs in total) in this cage and each one was marked with numbered stick plate. These pits were filled with loose soils in such a way that a 5-7 cm thick soil layer was on the eggs. The pits were covered with broad (palm) leaves during hot days to retain moisture in the soil. When topsoil of cage-II was too dry, water was added. Later on, some grasses grew naturally.

Hatching and Hatchability. After two months of incubation, several nests were excavated weekly to check for hatching and 2-5 eggs were opened to see the development of embryos (Fig. 4). Those hatched (Fig. 5) were immediately transferred into baby nursery. When sufficient number of hatchlings were obtained in cage-I, all the remaining eggs which seemed to be still alive were transferred into 7 big trays (0.5 m x 2.5 m x 0.25 m) in the nursery, these trays were kept separate from the hatched lizards by a wall of 1 m within the nursery. The earlier mentioned precautions were taken during this transfer. Eggs were placed half-buried in the tray soil with the usual cover. Each tray was checked twice a day (morning and late afternoon) and the number of hatchlings was recorded. Then hatchlings were released immediately in the nursery after careful noting of their measurements (Table 2).

Figure 3. Incubation cages for *Varanus bengalensis*. Cage I (left), Cage II (right). See text for description.

Table 1. *Varanus bengalensis* egg sizes (n=24).

Size	Mean ± SD	Range
Length (cm)	5.71 ± 0.41	4.92 - 6.18
Width (cm)	2.92 ± 0.06	2.80 - 3.04
Weight (gm)	26.93 ± 5.45	25.2 - 31.5

Baby Nursery. The concrete floor of the nursery (9.5 m x 3.6 m x 3 m) was covered with sandy loam soil. Tin sheets (40 cm high) were fitted against the nursery walls to prevent the escape of the baby lizards. Lumps of termite mounds containing termites (adults, mostly eggs and larvae) were placed in the periphery of the nursery as food for the hatchlings. Other foods offered to the babies were crushed boiled poultry eggs, minced beef and minced clean stomach of bovine. Two artificial small water reservoirs (25.4 cm x 25.4 cm x 5 cm) were made in the nursery.

All non-hatched eggs were piled and randomly 100 eggs from incubation cage-I and 150 from incubation cage-II were opened to determine the percentage of undeveloped eggs and dead embryos (Fig. 4).

Observations, Results, and Discussion

Food. Besides the supplied food, lizards were also seen to eat arthropods especially beetles and grubs from cow-dung, and small fish (mainly *Tilapia*, which were released in the lake for propagation).

Table 2. Size of hatchling *Varanus bengalensis* (n=39).

Size*	Mean ± SD	Range
Total length (cm)	19.72 ± 1.31	17.2 - 22.2
Body length (cm)	9.24 ± 0.59	8.3 - 10.4
Tail length (cm)	10.52 ± 1.02	7.5 - 12.5
Total weight (gm)	13.61 ± 3.73	8.3 - 22.1

* Total length (snout to tail tip), body length (snout to anus), and tail length (anus to tail tip).

Caring. Sick lizards were provided with food closer to them. Medical treatment was not given.

Eggs. Eggs were white, oval, with soft leathery skin and contained a large yolk supply. The farm staff collected a total of 20,499 eggs from the holes of termite mounds during 11 September to 30 October, 1995. Although the first clutch of eggs (18) were found on 10 August, 1995 inside a termite mound on the embankment of a pond inside the farm, this was not recorded by the farm staff (so it is excluded from the total count). The average collection of eggs was 512.67 + 134.49 (range 160-1210, n=38 days) per day.

Whitaker and Hikida (1981) and Akond et al. (1982) stated that the egg-laying period of Bengal lizard in Bangladesh is November and December. Daniel (1983), however, reported that eggs were collected from mid April to October in India. In Sri Lanka, the peak breeding period of Bengal lizard is January to April, but eggs also occur during June to December in ground logs or termite mounds (Deraniyagala, 1958). In the present study the egg-laying period was much earlier than that recorded by Whitaker and Hikida (1981) and Akond et al. (1982).

The mean size of egg was 5.71 cm in length, 2.92 cm in width and 26.93 gm in weight (Table 1). From India, Daniel (1983) reported that the average egg size of gray lizard was 4.9 x 3.8 cm (range 4.7 x 3.6 to 5.5 x 4.4 cm, n=50) and weighed 11.4 gm (range 8.3-14.3 gm, n=25). The size of eggs in this study (Table 1) is close to that reported by Daniel (1983), but the weight data are very different.

Clutch size. Clutch size varies according to the size and age of the females, larger and older females lay more eggs than younger and smaller ones. The average clutch size was 21.1 + 7.4 (range 10 - 32, n=25). The clutch size of Bengal lizard was 8-32 (Whitaker and Hikida,

Table 3. Minimum and maximum air temperatures and soil temperature (°C) during study period.

Month	Air		Soil	
	Minimum	Maximum	Morning	Late afternoon
November 1995	20.4	25.6	22.4	24.8
December 1995	18.0	22.4	18.0	22.1
January 1996	16.7	20.8	16.5	22.5
February	19.8	20.8	19.6	25.1
March	22.7	26.7	22.3	28.1
April	NR	NR	NR	NR
May	27.3	35.0	29.8	30.4
June	25.4	32.8	27.7	29.6

NR- Not recorded.

1981; Akond et al., 1982) and 20-30 (Khan, 1987) in Bangladesh, while 8-30 in India (Daniel, 1983). The range of present observation is close to the mentioned works except for Khan (1987).

Incubation period. On average, the incubation period of egg was 192.72 + 4.59 days (range 189-216 days, n=678 eggs). The first lizard hatched on 18 March and the last on 4 June, 1996. Most of the lizards hatched late at night or early in the morning; some also hatched during the day.

Previously recorded incubation periods for the Bengal Monitor Lizards of Bangladesh were 7-8 months (i.e., 210-240 days) (Whitaker and Hikida, 1981); 6-8 months (i.e. 180-240 days) (Akond et al., 1982) and 7-8 months (i.e. 210-240 days) (Khan, 1987). Daniel (1983) mentioned that the incubation period of Bengal lizard in India was 8-9 months (i.e. 240-270 days). The present incubation period is closer to that recorded by Whitaker and Hikida (1981) and Akond et al. (1982), but smaller than that reported by Daniel (1983). The egg-hatching month has been mentioned as July (Whitaker and Hikida, 1981) and June-July (Akond et al., 1982) while in the present observation it spreads over mid March to early June.

The variation in the incubation period of the present work and those of the above mentioned works could be due to the effect of some ecological factors like temperature, moisture, rainfall, etc. We recorded air temperature in the farm and soil temperature of nest of the incubation cage-I (and later baby nursery) which give an indication of these conditions (Table 3).

Hatchlings and hatching success. The average total length and weight of the hatchlings were 19.72 cm and 13.61 gm, respectively (Table 2). Out of 20,499 eggs, only 678 babies hatched. The hatching success, in this case, was 3.3%. (All the hatched eggs [678] were from cage-I only and the hatching success was 11.9%, but the eggs from cage-II resulted the poor hatching success i.e., 3.3%). After hatching out, a baby lizard did not eat for the next 2-3 days due to a continued absorbance of its yolk reserve. Neonate lizards ate termite eggs and larvae from the supplied lumps of termite mounds inside the

Figure 4. *Varanus bengalensis* in two stages of development: embryo (left), newly hatched (right).

Figure 5. *Varanus bengalensis* neonates.

nursery and crushed boiled poultry eggs from the feeding trays. They showed less interest to eat minced beef and minced bovine stomach. Babies also drank water and preferred to roost in cold, damp areas inside grasses or water hyacinths, which were kept in a few places inside the nursery.

The poor hatching success of eggs in this study was most probably due to: (1) soil in the incubation cage-II became compact due to rain and killed embryos; (2) mis-handling of eggs by the staff during egg transplantation; (3) unregulated temperature and moisture in the incubation cages. Of these reasons, the first one was most important because only 12 eggs hatched from the incubation cage-II (where 14,799 eggs were transplanted) and dead embryos or babies were found in 70% of the eggs (n=140). On the other hand, we were not sure whether all the unhatched eggs were fertilized or not. The additional reason for this huge damage of eggs was the negligence of the Managing Director of the project to implement our suggestions in constructing incubation cage-II.

Problems regarding farming

The following problems were faced during the study period:

1. The set up of the project is not well designed and scientific.
2. Lack of electricity.
3. Instructions/suggestions given (jointly by the advisor and consultant) to the Managing Director (MD) of the project were not properly followed.
4. Research facilities provided by the farm are poor.

Recommendations

1. Lizards should be caged rather than distributing them throughout the farm. A few small cages should be built for research.
2. Needs devoted staff.
3. Needs electricity.
4. Incubation cages should be constructed like cage-I.
5. Needs incubation chamber, or at least a place(s) where temperature and moisture fluctuaions are not drastic.
6. Needs separate "nursery" cages for neonates and juveniles.
7. Above all, instructions and suggestions proposed jointly by the advisor and consultant should be considered in all activities.

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A New Locality for the Rare Bornean Skink, *Lamprolepis vyneri* (Shelford, 1905) (Sauria: Scincidae)

INDRANEIL DAS

Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300, Kota Samarahan, Sarawak, Malaysia; E-mail: idas@ibec.unimas.my

Abstract. - A specimen of the Bornean arboreal skink, *Lamprolepis vyneri* (Shelford, 1905), hitherto known from the holotype from Gunung Balingan, Sibu Division, Sarawak, and a second possible specimen from the upper reaches of Sungei Mahakam, Kalimantan, is reported from Bukit Balian, near the Kayan settlement of Kelep, at Sungei Asap, at the base of Gunung Dulit, Kapit Division, Sarawak. The species is illustrated for the first time.

Key words. - *Lamprolepis vyneri*, redescription, Scincidae, Sarawak, Borneo.

Introduction

The genus *Lamprolepis* Fitzinger, 1843, which was revived from the synonymy of *Dasia* Gray (1829), by Greer (1970) contains four nominal species of arboreal skinks. Two of these are endemic to Borneo (*L. nieuwenhuisii* and *L. vyneri*), a third (*L. leucosticta*) to Java (Manthey and Grossmann, 1997:263) and the fourth (*L. smaragdina*) is widespread in the Philippines, Sulawesi, Lesser Sundas, the Republic of Belau, the Carolines, New Guinea, the Solomons and Santa Cruz Islands (Brown and Alcala, 1980:76-79; Greer, 1970). The first two species are arguably the least well known of all Bornean lizards. *L. nieuwenhuisii* (Lidth de Jeude, 1905) was described from "Long Bloe" (= Long Blu or Bloéoe, 00° 43' N; 114° 25' E), on the upper reaches of Sungei Mahakam, Kalimantan Tengah Province, Indonesia; RMNH 4455, holotype). It has subsequently been collected from isolated localities in northern Borneo, including Nanga Tekalit Camp on Sungei Mengiong, Kapit Division (reported as *Dasia vyneri* by Lloyd et al., 1968, based on FMNH 138542; 147562); and Pangkalan Lobang at Niah National Park, Miri Division (FMNH 131528), both in Sarawak State; and Kiau, Gunung Kinabalu National Park, Ranau District (MCZ 43494; BMNH 1929.12.22.96 and ZRC 2.1595); and Mahunbayon, Gunung Kinabalu National Park, Ranau District (MCZ 43495), both in Sabah State, East Malaysia.

Lamprolepis vyneri (Shelford, 1905) is more poorly known. Named for Charles Vyner Brooke (1874-1963), the Rajah Muda of Sarawak at the time of description of the species, and subsequently, the Third Rajah of Sarawak between 1917-1946, it is only known from the holotype, BMNH 1946.8.15.56 (ex-BMNH 1909.8.18.2), from "Mount Balineau, Muka district, Sarawak" (= Gunung Balingan, 01° 25' N; 111° 28' E, Sibu Division, East Malaysia), according to the original description. However, in the records of the Sarawak Museum (Anon., 1903), the type locality is given as "Mt. Balingean" (in Muka District, Sibu Division, Sarawak). Lidth de Jeude (1905) questionably assigned to this species a specimen from the upper reaches of Sungei Mahakam (00° 30' S; 117° 15' E), Kalimantan Timur Province, which apparently differed from Shelford's (1905) species in some trivial details of squamation and body proportions. The location of this specimen is unknown, but was examined by De Rooij (1915), who allocated it to the present species. This species has never been illustrated.

A second specimen (ZRC 2.5513; Figs. 1-2) of *Lamprolepis vyneri* is reported here from Bukit Belian (03° 08' 34.4" N; 113° 55' 45.5" E), near the Kayan settlement of Kelep, at Sungei Asap, situated at the base of Gunung Dulit, Kapit District, Sarawak. It was collected dead on 6 November 2001 from a logging road.

Material and Methods

The specimen was photographed upon collection, fixed in neutral buffered formalin and subsequently transferred to 70% ethanol, within a week of collection. The following measurements were taken with Mitutoyo™ dial caliper (to the nearest 0.1 mm): snout-vent length (SVL; from tip of snout to vent), tail length (TL; from vent to end of unregenerated tail; tip missing), tail width (TW; measured at base of tail); head length (HL; distance between posterior edge of last supralabial and snout-tip), head width (HW; measured at angle of jaws), head depth (HD; maximum height of head, from occiput to throat), ear length (EL; greater ear length); eye diameter (ED; greatest diameter of orbit), eye to nostril distance (E-N; distance between anteriormost point of eyes and nostrils), eye to snout distance (E-S; distance

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Figure 1. The Sungei Asap specimen of *Lamprolepis vyneri* (ZRC 2.5513), showing (left) general view of body and (right) close-up of head and forebody.

between anteriormost point of eyes and tip of snout), eye to ear distance (E-E; distance from anterior edge of ear opening to posterior corner of eyes), internarial distance (IN; distance between nares), interorbital distance (IO; shortest distance between orbits), tibia length (TBL; straight length of tibia, from knee to sole), in addition to measurements of digits, taken on the left limbs, from the base to tip. Scale counts and external observations of morphology were made using an Olympus SZX9 dissecting microscope. Institutional abbreviations follow Leviton et al. (1985), except ZRC is retained for USDZ, following conventional usage.

Description of *Lamprolepis vyneri* from Bukit Belian, Sungei Asap (ZRC 2.5513). - Habitus relatively slender, snout-vent length 55.2 mm; head elongate (HL/SVL ratio 0.20), narrow (HW/HL ratio 0.65), moderately depressed (HD/HL ratio 0.11), slightly distinct from neck; snout long (E-S/HW ratio 0.72), longer than the eye diameter (ED/E-S ratio 0.75), projecting slightly beyond mandible; interparietal distinct; parietal eye absent; supraoculars four; second and third largest; supraciliaries 8/8; first supraciliary contacts frontal; scales on snout and forehead smooth; rostral contact frontonasal posteriorly; rostral small, wider than deep (rostral width = 2.0 mm; rostral depth = 1.2 mm; width/depth ratio 1.67), contacted posteriorly by nasal and frontonasal; posteroventrally, rostral in contact with first supralabial; nares slit-like, situated on upper level of nasal, oriented laterally; nasal in broad contact with first supralabial; supranasals moderate in size, separated; frontonasal trapezoid, wider than long, contacting frontal and prefrontals posteriorly; frontal longer than frontonasal, not constricted laterally; frontoparietals in contact with each other and with three supraoculars, and posteriorly, with interparietal and parietals; a single pair of parietals contacts interparietal; parietals separated behind by an azygous scale; loreals two, anteriormost longer than deep; a small dorsal presubocular, and a wider ventral one; eye large (ED/HL ratio 0.35); postsuboculars two; supralabials seven, with supralabials 4-6 in suborbital position; supralabials three, fifth and sixth larger than the others; infralabials six; lower eyelid scaly; a single preocular between loreal and orbit; postoculars two; pretemporals two; two anterior and two posterior temporals; ear opening narrow, measuring 1.9 mm; situated laterally at a level slightly higher than jaws; a few lobules around ear opening present; tympanum deeply sunk; eye-to-ear distance less than eye-to-nostril distance (E-E/E-N ratio 1.26); a pair of enlarged nuchals, partially separated by a single cycloid scale; mental large, semicircular, wider than deep; postmental single, trapezoidal, larger than mental, its width 1.8 mm or 25.4 per cent head width; postmental contacts first infralabial only, bounded posteriorly by a pair of smooth, squarish, juxtaposed chin shields that are in contact; three pairs of enlarged chin shields, the first in contact with each other, the second separated by a single scale, the third separated by three scales; tongue narrowly elongate, narrowed distally, with a median cleft and scattered papillae on the dorsal surface; maxillary and mandibular teeth small, undifferentiated.

Body slender, elongate (SVL/BW ratio 6.81); dorsum and venter with smooth scales, with faint striae, scale size subequal dorsally as well as ventrally; anals six, smooth; outer overlapping inner; preanals three, not greatly enlarged, overlapped by last ventral, third preanal exceeding its posterior level, over vent; flank scales reduced in size.

Limbs well developed, pentadactyle; adpressed limbs meeting at level of heels; lamellae under finger IV numbering 18; lamellae under toe IV numbering 20; relative length of fingers (measurements in mm, in parentheses): 4 (4.5) > 3 (4.4) > 2 (3.5) > 5 (2.7) > 1 (2.0); relative length of toes: (measurements in mm, in parentheses): 4 (7.8) > 3 (5.6) > 5 (5.5) > 2 (4.7) > 1 (3.0).

Tail long, preserved tail length over 40.5 mm (tip missing), longer than snout-vent length; tail base slightly swollen; ventral surface of tail with smooth; subcaudals very wide; scales on the postanal region and at the proximal part of the tail base smooth.

Coloration. - Forehead olive-yellow, edged with black; dark smudges on forehead scales; scales on dorsum of

Figure 2. Head of *Lamprolepis vyneri* (ZRC 2.5513) in dorsal (left) and ventral (right) views. Scale bars = 10 mm.

Figure 3. Map of Borneo showing the known localities for *Lamprolepis vyneri*. 1 = Gunung Balingan, Sibu Division (type locality); 2 = Bukit Balian, near Sungei Asap, Kapit Division.

body bright yellow, edged with black, appearing as four dark longitudinal lines that extend along the body to slightly beyond the base of tail; yellow dorsolateral stripe, 2-3 scale wide, runs from behind level of the axilla, across the inguinal region, continuing along the side of the tail; venter, including the gular, pectoral and abdominal regions, undersurface of tail and of limbs yellowish-green, unpatterned; scales on flanks black-edged, reddish-orange, with scattered yellow scales; the same coloration is found on the upper surfaces of the fore and hind limbs; tail alternately banded yellowish-brown, each band one scale wide, and pale yellow; tongue and inner lining of mouth yellowish-pink; inner lining of body cavity yellowish-pink in preservative.

Measurements (in mm). - BW 8.1; ED 3.8; E-E 4.8; EL 1.2; E-N 3.8; E-S 5.1; IN 1.7; IO 4.5; HD 5.8; HL 10.9; HW 7.1; SVL 55.2; TBL 7.7; and TL 40.5 - original unregenerated, tip missing; TW 5.3.

Scutellation. - Ventrals (between postmental and preanal) 49; midbody scale rows 22; subcaudal count unknown (tail-tip missing); supralabials seven (fourth, fifth and sixth in suborbital position) and infralabials six.

Variation. - The Sungei Asap specimen differs from the holotype in the following particulars: SVL 55.2 vs 52.0 mm; supraoculars on left side four (vs five in the holotype, as shown on the apparently anomalous right side of the head of the Bukit Belian specimen). The bright red and yellow coloration of the flanks of the Bukit Belian specimen turned to dark brown after three months of storage in preservative. Shelford (1905), who presumably examined a preserved specimen, reported the flanks as being olive-gray. van Lidth de Jeude's (1905) specimen was 63 mm in SVL, and showed five black stripes, but only three entering the sacral region and tail-base. This poorly-preserved specimen was described as "putty grey", with several cephalic scales edged with black.

Notes on Natural History. - The specimen being reported here was found freshly dead on a logging track at the base of Bukit Belian (03° 08' 34.4" N; 113° 55' 45.5" E), near Kelep, Sungei Asap, a Kayan resettlement colony in Kapit (Seventh) Division, central Sarawak. It may have fallen off a log that was being transported, because the members of the genus are highly arboreal, and the present specimen was otherwise physically intact, except for the missing tail-tip, and not run over. The area lies within a lowland dipterocarp forest with strands of the Bornean ironwood tree, *Eusideroxylon zwageri* (Iban name: Belian, which gives the hill its name) at 186 m elevation. Perhaps coincidentally, the holotype was taken at a similar-sounding locality, Gunung Balingan, for which no general habitat description is available. One is therefore tempted to speculate

that both localities derive their names for their strands of the Bornean ironwood, a dipterocarp much in demand from the timber industry for its durability, and hence threatened by logging. The new locality, at the base of Gunung Dulit, is ca. 190 km east of the type locality, across the Lumut Range (Fig. 3).

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Leptobrachium smithi Matsui, Nabitabhata, and Panha, 1999 (Anura: Megophryidae), an Addition to the Fauna of Myanmar (Burma)

INDRANEIL DAS[1] AND SHYAMAL KUMAR CHANDA[2]

[1]*Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300, Kota Samarahan, Sarawak, Malaysia; E-mail: idas@ibec.unimas.my*

[2]*Amphibia Section, Zoological Survey of India, Fire-Proof Spirit Building, 27, J. L. Nehru Road, Kolkata 700 019, India*

Abstract. - Three specimens of *Leptobrachium* from the collections of the Zoological Survey of India are identified as *Leptobrachium smithi*. These specimens were collected by Limborg in 1877. These are the first confirmed records of *Leptobrachium smithi* for Myanmar.

Key words. - Anura, *Leptobrachium*, Myanmar, Burma.

Leptobrachium smithi Matsui et al. (1999) was described from peninsular Thailand, based on populations that were formerly referred to *L. hasseltii* Tschudi, 1838 (see Frost, 1985). This species was recently reported from Chandubi in the Mayeng Hill Reserve Forest and Garbhanga Reserve Forest, Kamrup District, Assam State, north-eastern India by Sengupta et al. (2001). We here report specimens from Myanmar in the collection of the Zoological Survey of India (ZSI) that are allocated to *L. smithi*.

Three specimens of *Leptobrachium smithii* were examined: ZSI 10439-40, from "Ahsoon" (unlocated), in Tenasserim, Myanmar, altitude "2,000 feet", collected by the Swedish journalist, novelist, poet and ship captain, Gustaf Arthur Ossian Limborg (1849-1908) in 1877. Limborg's expedition to what was then Burma was sponsored by Lord Tweeddale (Kjellgren, 1983) and his collections are distributed in Sweden and the US). Also examined was ZSI 11841, from Lampi Island, Mergui, collected by John Anderson, in 1882 (referred to by Anderson, 1889, as from "Sullivan Island", an older name for Lampi, 10° 50' N; 98° 15' E).

The material from Myanmar match the description of original description of *Leptobrachium smithi*, in addition to additional specimens examined from Assam State (see Sengupta et al., 2001), in showing the following characteristics: moderate body size (snout-vent length 22.4-43.4 mm; head width 6.6-18.1 mm; n = 3); small inner metatarsal tubercle; dorsum smooth; and absence of rows of dermal ridges on dorsal surface of limbs. All specimens referred to here are discolored, hence other characters used in separating *L. smithi* from *L. hasseltii*, such as absence of white spots on sides of body and on thigh; absence of dark spots on ventrum; and absence of dark markings on dorsum, that differentiates the northern *L. smithi* from the southern *L. hasseltii*, are indiscernable.

The known distribution of *Leptobrachium smithi* is thus north-eastern India, Myanmar (first country record on the basis of ZSI specimens reported here) and Thailand. Matsui et al. (1999) suspected the occurrence of the species in southern Myanmar, based of the larval description of *L. hassseltii* by Annandale (1917:153-157, as *Megalophrys hasseltii*), from the Dawna Hills of the Tenasserim. We have examined these specimens (ZSI 16735-43) that carry the following locality "Misty Hollow, w side of Dawna Hills, L. Burma". Surprisingly, Annandale, neither in his 1917 monograph, nor in any other works, have referred to the specimens from Burma mentioned earlier, although all of these were available to him (see Sclater, 1892).

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Species Diversity and Checklist of the Herpetofauna of Pulau Tioman, Peninsular Malaysia, With a Preliminary Overview of Habitat Utilization

Jesse L. Grismer[1], L. Lee Grismer[1], Indraneil Das[2], Norsham S. Yaakob[3], Lim Boo Liat[4], Tzi Ming Leong[5], Timothy M. Youmans[1], and Hinrich Kaiser[1]

[1]*Department of Biology, La Sierra University, Riverside, CA 92515-8247, USA*
[2]*Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan, Sarawak, Malaysia*
[3]*Forest Research Institute Malaysia, Kepong, 52109 Kuala Lumpur, Malaysia*
[4]*Taman Negara (PERHILITAN), Km 10 Jalan Cheras, 50664 Kuala Lumpur, Malaysia*
[5]*Department of Biological Sciences, National University of Singapore, Singapore 119260*

Abstract. - The environmental diversity of Pulau Tioman, a 48 km^2 island off the eastern coast of Peninsular Malaysia, supports a remarkably diverse herpetofauna (97 species) with 22 frogs, one caecilian, one non-marine turtle, 34 lizards, and 39 snakes. The majority of this herpetofauna (74%) occurs in lowland dipterocarp forests. Fifteen new island records and eight newly described, or as yet undescribed, species are reported, bringing the number of endemic species to at least 11.

Key words. - Pulau Tioman, Malaysia, herpetofauna, habitat diversity, checklist.

Introduction

Pulau Tioman (Tioman Island) is centrally located on the Sunda Shelf 38 km off the southeast coast of Peninsular Malaysia in the South China Sea (Fig. 1). Despite its small size of approximately 48 km^2, it supports a diverse array of habitats. The island's coastline and low-lying periphery is dominated by mangrove and coastal vegetative communities whereas inland areas support lowland dipterocarp forest on the alluvial foothills and hill dipterocarp forest at upper elevations (Latiff et al. 1999). Topographically, Pulau Tioman is characterized by steep mountainous terrain reaching 1,035 m in elevation. Exposed granitic outcroppings consisting of large boulders define much of the island's rugged interior and its slopes are cut by several fast-flowing, boulder-strewn streams. As discussed below, this environmental diversity contributes to the island's remarkable herpetological diversity with 23 amphibians, one non-marine turtle, 33 lizards, and 39 snakes now confirmed as present on the island (Table 1). This is in contrast to the relative depauperate herpetofauna of the surrounding islands of Tulai (Grismer et al., 2001b), Aur (Escobar et al., 2002a; Grismer et al., 2001a), Dayang (Wood et al., 2003), Pemanggil (Youmans et al., 2002), Sembilan and Seribuat (Wood et al. in prep), Sibu and Besar (Wood et al., 2004a,b) and Tinggi (Escobar et al., 2002b).

Prior to Hendrickson (1966a,b), no herpetofaunal survey had been undertaken on Pulau Tioman and only

Figure 1. Location of Pulau Tioman, West Malaysia, in the South China Sea.

limited accounts on particular taxa existed (i.e., Boulenger, 1912; Smith, 1930; de Haas, 1949). However, despite the thoroughness of Hendrickson (1966a,b) and subsequent efforts by Day (1990), Lim and Lim (1999), Hien et al. (2001), and Grismer et al. (2002a), the herpetofauna of this small island still

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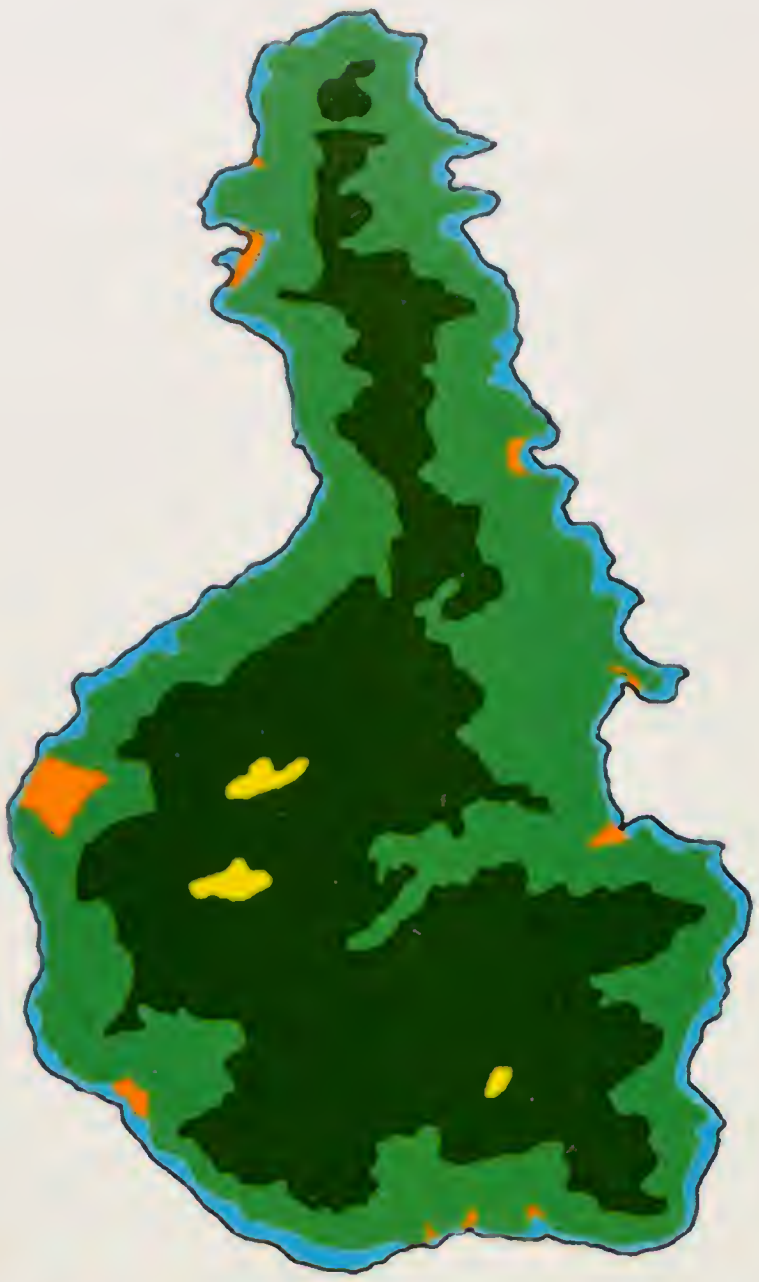

Figure 2. Distribution of vegetation zones on Pulau Tioman. Modified from Latiff et al. (1999).

remains incompletely known. This is evidenced by the 13 new island records since Grismer et al. (2002a) and Hien et al. (2001) and eight newly described and undescribed species reported herein. Additionally, there has been no attempt to establish the distribution or habitat use of each species on Pulau Tioman. Therefore, the intent of this paper is to report the results of the latest herpetofaunal surveys which not only list new additions to the island but new island localities of species known to be present. The latter will serve as the basis for a preliminary categorization of habitat use for each species based on its presence in different vegetation zones.

Figure 3. Mangrove swamp at Kampung Paya.

Vegetation Zones

Vegetation zones generally serve to highlight broad categorical differences between habitats across sizable geographic areas. On Pulau Tioman, as elsewhere, these categorical differences lack well-defined geographic boundaries (Ashton, 1995) and with the exception of mangrove communities, each zone transitions smoothly and continuously into another along an altitudinal transect. We use five different vegetation zones (Fig. 2), modified after Latiff et al. (1999), to characterize habitat differences on Pulau Tioman.

Mangroves (0 m; Fig. 3). - Mangrove swamps are disjunctly distributed along the island's coastline. Characteristic plant species include *Rhizophora apiculata*, *Bruguiear gymnorhiza*, *Excoecaria agallocha*, and *Avicennia alba*, which in some localities are unusually tall with large girth, attesting to the old age of the grove.

Coastal vegetation (0-80 m; Fig. 4). - Coastal vegetation forms a relatively narrow zone between the mangrove swamps (when present) and the lower reaches of the lowland dipterocarp forest. It is characterized by

Fig. 4. Coastal vegetation at Telok Nipah.

Fig. 5. Lowland dipterocarp forest on Tekek-Juara trail.

Fig. 6. Hill dipterocarp forest on Gunung Kajang.

Fig. 7. Ridge forest at summit of Gunung Kajang.

Figure 8. Collecting localities on Pulau Tioman. G. = Gunung (mountain); Kg. = Kampung (village); S. = Sungai (river); Tk. = Telok (bay); U. = Ulu (headwater).

palms, such as *Pandanus dubius*, and moderately-sized trees such as *Scaevola taccada*, *Calophyllum inophyllum*, and *Vitex trifolia*. Dipterocarp trees are noticeably absent.

Lowland dipterocarp forest (80-300 m; Fig. 5). - Lowland dipterocarp forest occurs on the alluvial slopes between coastal vegetation and hill dipterocarp forest and is usually dominated by large non-dipterocarp trees such as *Arenga pinnata*, *Caryota mitis*, and *Nenga macrocarpa*. A few large dipterocarp species such as *Anisoptera curtisii* and *Neobalanocarpus heimii* exist as emergents.

Hill dipterocarp forest (300-950 m; Fig. 6). - This zone is situated immediately above and adjacent to the lowland dipterocarp forest with which it is continuous. The transition from lowland dipterocarp forest to hill dipterocarp forest at approximately 300 m is essentially imperceptible and many plant species common to the lowland dipterocarp forest occur at lower elevations in the hill dipterocarp forest, a pattern paralleled by some species of amphibians and reptiles. To illustrate this we use the term low hill dipterocarp forest (300-500 m) and high hill dipterocarp forest (500-950 m). Hill dipterocarp forest is dominated throughout by large species of *Shorea* and *Dipterocarpus*.

Ridge forest (hill top summits between 950-1035 m; Fig. 7). - Ridge forest occurs on summits where mosses, ferns, lichens, and bryophytes predominate. Due to increased exposure to sun and wind, trees are relatively short. At this altitude, species such as *Garcinia penangiana*, *Licuala tiomanensis*, and *Scleria sumatrensis* dominate and presumably have adapted to live in the damp wind-blown environment typical of ridge forests.

Materials and Methods

Our data were collected from various localities (Fig. 8) on five trips; 12-24 March and 7-16 July, 2001 and 19-27 March, 13-21 July, and 6-19 August, 2002 unless indicated otherwise. Individuals sighted but not collected or photographed are listed but considered to be unconfirmed records. Collecting was done during the day by hand and blowpipes and at night by torch light. During July 2001 and 2002, three pitfall trap arrays with three 15-m drift fence sections at each array were stationed in lowland dipterocarp forest at 142 m and 241 m along the Tekek-Juara trail. A third array was estab-

Table 1. Species checklist and vegetation zone utilization of the amphibians and reptiles of Pulau Tioman. Data are derived from Hendrickson (1966a,b), Day (1990), Lim and Lim (1999), Grismer et al. (2002a) and this report. M = Mangrove; CV = Coastal vegetation; LD = Lowland dipterocarp forest; LHD = Low hill dipterocarp forest; HHD = High hill dipterocarp forest; and RF = Ridge forest; * = Species is endemic.

	M	CV	LD	LHD	HHD	RF
Megophryidae						
*Leptolalax kajangensis**				X	X	X
Megophrys nasuta			X	X	X	
Bufonidae						
*Ansonia tiomanica**			X	X	X	X
Bufo asper		X	X			
Bufo melanostictus		X	X			
Bufo parvus		X	X			
Pelophryne brevipes					X	X
Microhylidae						
Chaperina fusca		X	X	X		
Kalophrynus pleurostigma			X	X	X	
Kaloula baleata		X				
Kaloula pulchra		X	X			
Ranidae						
Fejervarya cancrivora	X	X		X		
Limnonectes blythii		X	X			
Limnonectes hascheanus			X			
Rana chalconota		X	X	X		
Rana erythraea	X	X				
Rana hosii			X	X		
Rana picturata			X			
Rhacophoridae						
Nyctixalus pictus			X	X		
Philautus petersi					X	X
Polypedates leucomystax		X	X	X		
Theloderma horridum			X			
Ichthyophiidae						
Ichthyophis sp.			X			
Trionychidae						
Dogania subplana		X	X	X		
Agamidae						
Acanthosaura armata		X	X	X	X	

Table 1. Continued

	M	CV	LD	LHD	HHD	RF
Agamidae						
Aphaniotis fusca			X	X		
Bronchocela cristatella		X	X	X		
Draco fimbriatus		X	X			
Draco haematopogon					X	
Draco melanopogon		X	X	X	X	
Draco sumatranus	X	X	X			
Gonocephalus chamaeleontinus			X	X	X	
Gonocephalus grandis			X	X		
Gekkonidae						
Cnemaspis kendallii		X	X	X		
Cnemaspis limi		X	X	X	X	X
Cosymbotus craspedotus		X	X			
Cosymbotus platyurus		X				
Cyrtodactylus quadrivirgatus			X	X	X	
*Cyrtodactylus tiomanensis**		X	X	X	X	
Gehyra mutilata			X			
Gekko monarchus		X	X			
Gekko smithii			X	X		
Hemidactylus frenatus		X				
Lepidodactylus lugubris		X				
Ptychozoon kuhli		X	X	X		
Scincidae						
Dasia olivacea		X	X	X	X	
Emoia atrocostata	X					
Eutropis longicaudata		X				
Eutropis multifasciata		X	X	X		
*Larutia seribuatensis**					X	
Lipinia surda		X	X			
Lipinia vittigera		X	X	X		
Lygosoma bowringii		X	X			
Sphenomorphus scotophilus		X	X	X	X	X
Sphenomorphus sp.*				X	X	X
Varanidae						
Varanus nebulosus		X	X			
Varanus salvator	X	X				

Table 1. Continued

	M	CV	LD	LHD	HHD	RF
Dibamidae						
*Dibamus tiomanensis**	X	X	X			
Typhlopidae						
Ramphotyphlops albiceps			X			
Ramphotyphlops braminus	X	X				
Pythonidae						
Python reticulatus	X	X	X			
Colubridae						
Ahaetulla prasina		X	X	X	X	
Boiga cynodon		X	X			
Boiga drapiezii			X	X		
Boiga nigriceps		X	X	X		
*Calamaria ingeri**				X		
Calamaria lumbricoidea			X	X	X	X
Calamaria pavimentata			X			
Cerberus rynchops	X			X		
Chrysopelea pelias			X			
Dendrelaphis caudolineatus		X	X			
Dendrelaphis cyanochloris			X			
Dendrelaphis pictus		X	X			
Denderlaphis striatus		X	X			
Dryocalamus subannulatus		X	X			
Dryophiops rubescens		X	X			
Elaphe flavolineata		X				
Elaphae taeniura		X	X			
Enhydris enhydris	X	X				
Enhydris plumbea	X	X				
Fordonia leucobalia	X	X				
*Gongylosoma mukutense**		X	X			
Gonyosoma oxycephalum	X	X				
Lepturophis albofuscus			X			
Liopeltis tricolor			X	X	X	
Oligodon purpurascens			X	X	X	
*Oligodon booliati**			X	X	X	
Pareas vertebralis					X	X
Psammodynastes pulverulentus	X	X	X	X	X	

Table 1. Continued

	M	CV	LD	LHD	HHD	RF
Colubridae						
Ptyas carinatus		X	X	X	X	
Rhabdophis chrysargos	X	X	X			
Sibynophis melanocephalus		X				
Elapidae						
Bungarus flaviceps			X			
Calliophis intestinalis			X			
Ophiophagus hannah	X	X				
Viperidae						
Trimeresurus sp.*			X			
Unconfirmed Species						
Chrysopelea paradisi						
Naja sumatrana						

lished on the beach near boulders in coastal vegetation 1 km south of Kampung Tekek. Collecting site elevations were estimated with the aid of a hand-held global positioning satellite unit. Distribution data for species not addressed in the accounts below but listed in Table 1 were taken from Lim and Lim (1999).

Representatives of all species collected were photographed, tissued for liver, preserved, and deposited in the Department of Wildlife (PERHILITAN; JAM cat. nos.), Kulala Lumpur, Malaysia; Forest Research Institute of Malaysia (FRIM), Kulala Lumpur, Malaysia; the Zoological Reference Collection (ZRC) of the Raffles Museum of Biodiversity Research at the National University of Singapore; and the La Sierra University Herpetological Collection (LSUHC), Riverside, California, USA. Material from Hendrickson's (1966a,b) collection deposited in the Bishop Museum (BPBM), Honolulu, Hawai'i and Day's (1990) collection (uncatalogued in the British Museum of Natural History, London) was also examined. All tissues have been deposited at La Sierra University. Photographs are catalogued in the La Sierra University Photographic Collection (LSUPC) in the herpetology laboratory of L. Lee Grismer. The taxonomy of ranid genera follows Inger and Voris (2001).

Annotated Checklist

Amphibia

Order: Anura

Family: Megophryidae

Leptolalax kajangensis Grismer, Grismer, and Youmans, 2004
(Fig. 9)

Localities. - Larvae collected from 400 m on Gunung Kajang were reported by Lim and Lim (1999). Day (1990) reported larvae from a pool at Gua Tengkuk Air at 845 m. On 19 March 2001, we collected two adults (ZRC 1.7714-15) from Gua Tengkuk Air sitting on boulders approximately 2 m from the water 10 m below the surface of the cave floor. On 23 March, 2001, a specimen (LSUHC 4431) was collected from a cave at the summit of Gunung Kajang at 1035 m. On 10 August, 2002 and adult female (LSUPC-F1497) was observed at 210 m elevation along the Tekek-Juara trail. This species occurs from lowland dipterocarp to ridge forests. This species was originally known only from tadpoles and was reported as *Leptobrachium* sp. (Day, 1990) and *Leptolalax gracilis* (Lim and Lim, 1999). Examination of the adults indicated they belonged to the new species *Leptolalax kajangensis* (Grismer et al., 2004).

Family: Bufonidae

Ansonia tiomanica Hendrickson, 1966
(Fig. 10)

Localities. - Gua Sinah at Ulu Lalang (800 m; Hendrickson, 1966b).

New localities. - On 3 November, 2000, a specimen (LSUPC-F439-45) was photographed sitting on the vertical surface of a rock near the top of the Tekek-Juara trail at 220 m. On 19-21 March, 2001, we observed approximately 10 specimens in Gua Tengkuk Air at 845 m on Gunung Kajang. All were climbing on large boulders both in and outside of the cave. This species ranges from lowland dipterocarp to high hill dipterocarp forest in association with boulders in the vicinity of water.

Bufo asper Gravenhorst, 1829

Localities. - Sungai Nipah (80-200 m; Day, 1990).

New localities. - On 21 March 2001, we observed a specimen (LSUPC-F380-81) along the Sungai Mentawak (ca. 195 m) along the water's edge on a downward sloping face of a boulder. On 23 March, 2002, we observed 11 specimens during the day and night sitting on rocks at the edge of and within the Sungai Mentawak of which three (LSUHC 4443, 4447-48) were collected. This species occurs in coastal vegetation and lowland dipterocarp forest.

Bufo melanostictus Schneider, 1799

Localities. - Kampung Tekek (Lim and Lim, 1999).

New localities. - On 7 July, 2001, we collected specimens from Kampung Mukut (ca. 10 m) and on 9 July additional specimens (LSUHC 3754; ZRC 1.8248-49) were collected from the beginning of the Tekek-Juara trail (ca. 80 m) on the forest floor. On 9 July, 2001, a specimen (LSUHC 3814) was collected beneath a board at Kampung Paya (ca. 15 m). This species ranges from coastal vegetation to lowland dipterocarp forest.

Bufo parvus Boulenger, 1877

Localities. - Sungai Paya; Kampung Juara; and Sungai Keliling (Lim and Lim, 1999).

New localities. - Two specimens (JAM 1860-61) from Kampung Tekek were collected on 6 November, 1997. Additional specimens (LSUHC 3969-71, 3976-77, 3981; ZRC 1.8269) were collected on 11-17 July 2001 from the Tekek-Juara trail pitfall traps (142 m) and from Telok Dungun (ca. 25 m; ZRC 1.8263) on 12 July, 2001. This species ranges from coastal vegetation to lowland dipterocarp forest.

Family: Microhylidae

Chaperina fusca Mocquard, 1892

Localities. - Sungai Air Besar; Teluk Penut; and between Kampung Tekek and Kampung Lalang (Denzer et al., 1989: 27).

New localities. - On 10 July, 2001, a specimen (LSUHC 3833) was collected from Telok Nipah (ca. 20 m) under a flat rock at the edge of a narrow stream. At Telok Penut, tadpoles were also collected from deep holes in rocks located along the shore of a dried-up stream bed on 9 July, 2001 and were observed along the Tekek-Juara Trail in root holes, tree cavities, and pitfall traps from 200-245 m elevation. On 7 July, 2002 adults (LSUHC 4667-71) and tadpoles were found in water catchments within fallen palm fronds along the Sungai Mentawak at 195 m. This species ranges from coastal vegetation to low hill dipterocarp forest.

Kalophrynus pleurostigma Tschudi, 1838
(Fig. 11)

Localities. - Gunung Kajang trail at 245 m in elevation (Escobar et al., 2003).

New localities. - On 17 July, 2002, a specimen (LSUHC 4682) was collected at 200 m elevation along the Tekek-Juara trail. On 9 August, 2002, a specimen (LSUHC 5024) was collected at night on Gunung Kajang at 813 m as it was ascending the vertical surface of a small rock. This species ranges from lowland dipterpcarp to high hill dipterocarp forests.

Family: Ranidae

Fejervarya cancrivora Gravenhorst, 1829

Localities. - Kampung Lalang and Kampung Tekek (Hendrickson, 1966b).

New localities. - On 12 July, 2001, a specimen was collected at Telok Dalam (ca. 10 m) and released. The individual was sitting approximately 1 m from the edge of the water. When approached another specimen jumped into the water and buried itself in leaf liter at the bottom of the stream. This species occurs in mangroves and coastal vegetation.

Limnonectes blythii Boulenger, 1920

Localities. - Sedagong; Sungai Air Raja at Kampung Genting; Sungai Durian Kallang at Kampung Paya; Sungai Besar waterfall along Tekek-Juara trail; Sungai Pasal; Sungai Keliling; Sungai Paya; Sungai

Baharu; and Tekek-Juara trail (Lim and Lim, 1999).

New localities. - We add an additional specimen (LSUHC 3832) from Sungai Raya (ca. 100 m) collected on 10 July, 2001 and from the Sungai Mentawak (LSUHC 4642; 195 m) collected on 19 July, 2002. Both specimens were sitting near the water's edge on a large rock at night. Additonal speciemens (LSUHC 4646-47) were collected from a small stream at the back of Telok Monkey (ca. 3 m) on 19 July, 2002. This species occurs in coastal vegetation and lowland dipterocarp forest.

Limnonectes hascheanus Stoliczka, 1870

Localities. - Sungai Paya (Leong, 2000); Tekek-Juara Trail, Ulu Lalang (Hendrickson, 1966b).

New localities. - On 11 July, 2001, three specimens (LSUHC 3856, 3864, 3868) were collected from the Sungai Besar waterfall on the Tekek-Juara trail (220 m) while sitting near the base of the waterfall on a rocky slope. On 13 July, 2001, a specimen of *L. hascheanus* was observed but not collected at Telok Dalam. On 12 July, 2001 a specimen (LSUHC 3887) was collected from Sungai Dungun (ca.10 m). Hendrickson (1966b) reported two specimens of this species as "*Rana (Discodeles/Platymantis)* sp." Upon examination of his material (BPBM 14200-2001) we find them to be *L. hascheanus*. This species occurs in lowland dipterocarp forest.

Rana chalconota Schlegel, 1837-1844

Localities. - Tekek-Juara trail; Kampung Tekek; Sungai Keliling; Sungai Mentawak; and Sedagong (Lim and Lim, 1999).

New localities. - On 21 March, 2001, a juvenile (LSUPC-F285) was observed sitting on a leaf approximately 0.5 m above the ground behind a house in Kampung Juara (5 m). On 9 July 2001, three specimens (LSUHC 3803-05; ZRC 1.8255) were collected from Sungai Nipah (10 m). All were found inside large boulder caves situated within the stream. On 12 July, 2001, three specimens (LSUHC 3886, 3909-10) were collected from Telok Dungun (15 m). This species ranges from coastal vegetation to low hill dipterocarp forest.

Rana erythraea Schlegel, 1837-1844

Localities. - Kampung Tekek (Hendrickson, 1966b).

New localities - On 9 July, 2001, a specimen (LSUHC 3815) was collected at sea level from Kampung Paya from along a large pond just behind the beach. On 21 March, 2002, one specimen was found during the day sitting on the branch of a mangrove tree 1 m above the water at Air Batang (ca. 5 m). This species occurs in mangrove and coastal vegetation.

Rana hosii Boulenger, 1891

Localities. - Tekek-Juara trail; Kampung Paya; Sungai Kalang; and Sungai Ayer Besar waterfall on the Tekek-Juara trail (Lim and Lim, 1999).

New localities. - On 13 July, 2001, a specimen was observed along Sungai Dungun, but not collected. On 11 July, 2001, a specimen (LSUHC 3819) was collected along Sungai Raya (ca. 50 m). On the evening of 19 July, 2002, three specimens (LSUHC 4625-26) were collected along the Sungai Mentawak at 195 m in elevation while sitting on vegetation. This species occurs in lowland dipterocarp and low hill dipterocarp forest.

Rana picturata Boulenger, 1920
(Fig. 12)

Localities. - Tributary of Sungai Mentawak (Day, 1990).

New localities. - Day (1990) reported a specimen *Rana signata* from a tributary of the Sungai Mentawak at 300 m. We have examined that specimen (uncatalogued in the British Museum of Natural History) and find it to be *R. picturata*. We report additional specimens of *R. picturata* from the Sungai Mentawak at 195 m collected on 24 March, 2002 (LSUHC 4435-41) and 19 July, 2002 (LSUHC 4636-40). All were found perched on rocks or vegetation along the water's edge during the evening. This species is found in coastal and lowland dipterocarp forest.

Family: Rhacophoridae

Nyctixalus pictus Peters, 1871
(Fig. 13)

Localities. - A single specimen (ZRC 1.8268) was collected from the Tekek-Juara trail (ca. 240 m) on the night of 16 July, 2001 (Leong and Crane, 2002). It differs from other populations of *N. pictus* in that its body and limbs are yellow in coloration instead of orange or brownish. Another specimen was heard calling on 14 July, 2001 along a small stream on the Tekek-Juara trail (ca. 100 m) by LBL and NSY. This specimen constitutes a new record for Pulau Tioman. This species occurs in lowland dipterocarp forest.

Polypedates leucomystax Boie, 1829

Localities. - Kampung Tekek and Kampung Juara (Lim and Lim, 1999).

New localities. - On 7 July, 2001, a specimen (LSUHC 3770) was collected on the Tekek-Juara trail (241 m) while sitting on a leaf approximately 1 m above the ground. On 11 July, 2001, a specimen was observed in the Sungai Dungun (ca. 10 m) but not collected. This species ranges from coastal vegetation to low hill dipterocarp forest.

Theloderma horridum Boulenger, 1903
(Fig. 14)

Localities. - On the evening of 22 March, 2002, one specimen of *Theloderma horridum* was found on the side of a large tree (ca. 1 m in diameter) near the Tekek-Juara trail at 245 m in elevation (Grismer et al. 2003a). On 14 July, 2002, another specimen was found on the Tekek-Juara trail at 140 m elevation. This species is found in lowland dipterocarp forest.

Reptilia
Order: Squamata
Family: Agamidae

Acanthosaura armata Hardwicke and Gray, 1827

Localities. - Tekek-Juara trail (Hendrickson, 1966b). .

New localities. - On 13 July, 2001, a specimen (LSUHC 3873) was collected in primary forest south of Kampung Salang (ca.80 m). On 18 March, 2001 two specimens were observed at Gua Tengkuk Air on Gunung Kajang at 845 m. One was photographed (LSUPC-L7070-71). The latter specimens had patterns that were considerably darker than those of specimens from lowland forests which appears to be a function of substrate matching. On 17 July, 2002, two specimens were collected at Telok Monkey (ca. 40 m). One (LSUHC 4598) was 1 m above ground level on a small (ca. 10 cm in diameter) tree facing head-up. The other (LSUHC 4599) was observed sitting on a hollow log that was lying on the forest floor. When approached, it ran into the hollow of the log in an attempt to escape. This species ranges from coastal vegetation to high hill dipterocarp forest.

Aphaniotis fusca Peters, 1864

Localities. - Sedagong; Tekek-Juara trail; Kampung Asah (Lim and Lim, 1999).

New localities. - On 18 March, 2001, an individual was photographed (LSUPC-L5931-36) and released on Gunung Kajang at 320 m in elevation. On 12 July, 2001, a male and female (LSUHC 3897; ZRC 2.5147) were collected from Telok Dalam off the same tree, facing head up approximately 1.5 m above the ground at 20 m. On 9 July, 2001, a sighting was made at Sungai Benuang at 15 m. On 9 July, 2001, an individual (LSUHC 3818) was collected from a tree in Kampung Mukut and another (ZRC 2.5131) from a sapling approximately 0.5 m above the ground at Telok Nipah at 20 m. This species ranges from lowland dipterocarp to low hill dipterocarp forest.

Bronchocela cristatella Kuhl, 1820

Localities. - Tekek-Juara trail near Kampung Juara; Kampung Juara; Kampung Tekek; and Kampung Mukut (Lim an Lim, 1999).

New localities. - On 19 July, 2000, a specimen was photographed (LSUPC-L762) at Kampung Air Batang at 15 m. On 13 July, 2001, a specimen was observed from primary forest in Telok Dalam at 15 m. On 18 July, 2002, one specimen (LSUHC 4613) was observed on a tree in coastal forest at Telok Monkey (ca. 20 m). On 11 August, 2002, a specimen (LSUHC 5046) was collected from 15 m above ground level on a branch at the base of Gunung Kajang at 291 m in elevation. This species occurs from coastal vegetation to low hill dipterocarp forest.

Draco fimbriatus Kuhl, 1820
(Fig. 15)

Localities. - On 8 July, 2001, a specimen (ZRC 2.5130) was collected from a large dipterocarp tree approximately 6 m above the ground at 160 m on the Tekek-Juara trail. On 9 July, 2001, a second specimen (LSUHC 3823) was collected approximately 4 m above the ground at 142 m on the same trail. On 17 July, 2002, a male and female were observed 20 m above ground level on the side of a tree in coastal vegetation at Telok Monkey (ca. 20 m). The male (LSUHC 4601) was collected. These specimens constitute new island records. This species occurs in coastal vegetation and lowland dipterocarp forest.

Draco haematopogon Boie, 1831
(Fig. 16)

Localities. - On 20 March, 2001, an adult male (SVL 106 mm) and female (SVL 100 mm) were collected, photographed (LSUPC-L7072-78), and released from near Gua Tengkuk Air on Gunung Kajang at 845 m. The male had a yellow dewlap with a black spot at base surrounded by orange and the female had an orangish dewlap with a yellow fringe. Both were found on a large dipterocarp tree facing head up approximate-

Fig. 9. *Leptolalax kajangensis* from Gua Tengkuk Air, Gunung Kajang.

Fig. 10. *Ansonia tiomanica* from Tekek-Juara trail.

Fig. 11. *Kalophrynus pleurostigma* from the Tekek-Juara trail.

Fig. 12. *Rana picturata* from the Sungai Mentawak.

Fig. 13. *Nyctixalus pictus* from the Tekek-Juara trail.

Fig. 14. *Theloderma horridum* from the Tekek-Juara trail.

Fig. 15. *Draco fimbriatus* from the Tekek-Juara trail.

Fig. 16. *Draco haematopogon* from Gua Tengkuk Air, Gunung Kajang.

Fig. 17. *Cnemaspis limi* from the Tekek-Juara trail.

Fig. 18. *Crytodactylus tiomanensis* from the Tekek-Juara trail.

Fig. 19. *Lipinia vittigera* from Salang.

Fig. 20. *Sphenomorphus* sp. from the summit of Gunung Kajang.

Fig. 21. *Ramphotyphlops albiceps* from the Tekek-Juara trail.

Fig. 22. *Calamaria ingeri* from the Tekek-Juara trail.

Fig. 23. *Chrysopelea pelias* from the Tekek-Juara trail.

Fig. 24. *Dendrelaphis striatus* from Teluk Monkey.

Fig. 25. *Fordonia leucobalia* from Kampung Tekek.

Fig. 26. *Gongylosoma muketense* from Kampung Mukut.

Fig. 27. *Gonyosoma oxycephalum* from Kampung Juara. Photo by Pauli Hien.

Fig. 28. *Oligodon purpurescens* from the Gunung Kajang trail.

Fig. 29. *Rhabdophis chrysargos* from the Tekek-Juara trail.

Fig. 30. *Sibynophis melanocephalus* from Kampung Juara.

Figure 31. *Trimeresurus* sp. (male) from Tekek-Juara trail.

ly 6 m above the ground. These specimens constitute a new island record. This species occurs in high hill dipterocarp forest.

Draco melanopogon Boulenger, 1887

Localities. -Tekek-Juara trail; Sedagong; Kampung Asah; Kampung Paya; and Gunung Kajang at 800 m (Lim an Lim, 1999).

New localities. - On 9 and 11 March, 2001, respectively, a specimen (LSUHC 3809) was colleted from Telok Nipah (10 m) and Sungai Nipah (LSUHC 3869) at 20 m. Day (1990) reported an unidentified species of *Draco* at Telok Nipah based on his sighting of two individuals with pinkish dewlaps displaying at one another. We observed individuals with pinkish dewlaps at Telok Nipah and elsewhere to be female *D. melanopogon*. On 13 July, 2001, a specimen (LSUHC 3908) was collected at Telok Dalam in primary forest at 20 m. On 12 July, 2001, several specimens were observed at Telok Dungun at 10-35 m. On 13 July, 2001, a specimen (LSUHC 3903) was collected at Kampung Salang at 10-15 m. Two specimens (LSUHC 3798, 3809) were collected from Sungai Benuang (10 m) and one (LSUHC 3822) from Sungai Raya on 9 July, 2001 at 40 m. One specimen (LSUHC 5021) was collected on Gunung Kajang at 813 m on 8 August, 2002. This species ranges from coastal vegetation to high hill dipterocarp.

Draco sumatranus Schlegel, 1844

Localities. - Kampung Tekek; Sungai Mukut at Kampung Mukut; and Kampung Air Batang (Lim and Lim, 1999).

New localities. - On 9 March, 2001, a male with a blue head was collected from Sungai Nipah at approximately 20 m. On 8 July, 2001, two specimens (LSUHC 3777; ZRC 2.5121) were collected from the Tekek-Juara trail in lowland forest at 80-150 m. On 12 July, 2001 an individual (LSUHC 3899) from Telok Dalam was found during mid-day in the mangroves approximately 3 m above ground. On 13 July, 2001, a specimen (LSUPC-L3103-04) was photographed at Telok Dungun at an elevation of 15 m. On 13 July, 2001, an individual was observed in coastal vegetation at Kampung Salang at approximately 10 m in elevation. All lizards were found facing head-up on trees. This species ranges from mangrove to lowland dipterocarp forest.

Gonocephalus chamaeleontinus Laurenti, 1768

Localities. - Tekek-Juara trail, Kampung Paya along the trail to Gunung Kajang (Lim and Lim, 1999).

New localities. - On 9 July, 2001 an individual was observed on Sungai Benuang at 15 m. On 10 July, 2001, a specimen (LSUHC 3881) was found at Telok Dungun in primary forest at 20 m. On 13 July, 2001, a specimen was observed from Kampung Salang in primary forest at 10 m. On 19 July, 2002, two specimens (LSUHC 4623-24) were observed at night sleeping on vegetation ca. 5 m above ground level along the Sungai Mentawak at 195 m. On 10 August, 2002, a specimen was observed on a small tree at Gua Tengkuk Air on Gunung Kajang at 845 m. All were found 2-5 m above the ground on the side of trees facing head-up. This species occurs from lowland dipterocarp to high hill dipterocarp forest.

Gonocephalus grandis Gray, 1845

Localities. - Sungai Asah; Sungai Nipah; Sedagong; and Sungai Air Besar (Lim and Lim, 1999).

New localities. - On 11 July, 2001, a male and a juvenile were sighted on trees along the Sungai Raya but not collected. On 15 July, 2001, a adult male was collected from a trail behind and leading out of Kampung Tekek. On 19 July, 2002, four specimens (LSUHC 4619-22) were observed on trees near the edge of Sungai Mentawak at 195 m. Additional specimens were observed on trees along a small stream at 291 m at the base of Gunung Kajang. This species ranges through lowland dipterocarp to low hill dipterocarp forests primarily in association with streams.

Family Gekkonidae

Cnemaspis kendallii Gray, 1845

Localities. - Tekek-Juara trail (Lim and Lim, 1999).

New localities. - On 18 March, 2001, individuals were observed at the base of Gunung Kajang and along the Sungai Mentawak (80-200 m). Additional specimens (LSUHC 3797) were collected at Sungai Benuang (9 July, 2001; LSUHC 3797; ca. 20 m), Kampung Paya (9 July, 2001; LSUHC 3811; ca. 15 m), Sungai Raya (11 July, 2001; LSUHC 3820; ca. 12 m), Kampung Salang (12 July, 2001; LSUHC 3878; ca. 10 m), and Telok Dalam (12 July, 2001; observed only). Additional specimens were found at Mukut (15 July, 2002; LSUHC 4566; ca. 50 m) and Telok Monkey (18 and 29 July, 2002; ca. 35 m; LSUHC 4615 and 4666, respectively). All were found on rocks or trees during both day and night. This species ranges from coastal vegetation to low hill dipterocarp forest.

Cnemaspis limi Das and Grismer, 2003
(Fig. 17)

Localities. - Tekek-Juara trail; Gunung Rokam; Gunung Kajang at 950 m (Lim and Lim, 1999).

New localities. - On 19 March, 2001, specimens (LSUPC-L3662-65) were photographed at Gua Tengkuk Air on Gunung Kajang at 845 m and from the summit at 1035 m. On 10 July, 2001, three specimens (LSUHC 3888, 3902; ZRC 2.5149) were collected in primary forest at Kampung Salang at 20 m. On 11 July, 2001, a specimen was observed at Telok Dungun at 100 m. On 9 July, 2001, a specimen was observed at the Sungai Raya at 25 m. On 17 and 18 July, 2002, two specimens (LSUHC 4596, 4616) were collected off rocks at Telok Monkey (ca. 20 m). On 19 July, 2002, one specimen (LSUHC 4629) was collected from the Sungai Mentawak at 195 m. The Pulau Tioman population was originally reported as *C. nigridia* (Hendrickson, 1966a) but was described as a new species (Das and Grismer, 2003) All specimens were observed on steep faces of large boulders in shaded areas or within deep rock crevices. This species occurs from coastal vegetation to ridge forest.

Cosymbotus craspedotus Mocquard, 1890

Localities. - On 9 November, 1997, a single specimen (JAM 1834) was collected from the palm groves in Kampung Tekek at the base of the Tekek-Juara trail at 50 m while facing head down approximately 3 m above the ground. This constitutes a new island record. This species occurs in coastal vegetation.

Cosymbotus platyurus Schneider, 1792

Localities. - Kampung Tekek (Grismer et al., 2002a).

New localities. - On 13 July, 2001, a juvenile (ZRC 2.5146) was collected in a restaurant on the beach at Kampung Salang. This species occurs in coastal vegetation.

Cyrtodactylus quadrivirgatus Taylor, 1962

Localities. - No locality data provided (Manthey and Grossmann, 1997:228).

New localities. - On 2 November, 2000, a specimen was observed and photographed (LSUPC-L3313) while sitting on a leaf approximately 1.5 m above the ground along the Tekek-Juara trail at 190 m. On 19 2001 March, a single specimen was observed at Gua Tengkuk Air on Gunung Kajang at 845 m. One specimen (LSUHC 5622) was collected off vegetation along the Sungai Mentawak

at 195 m on 7 August, 2002. This species ranges from lowland dipterocarp to high hill dipterocarp forest.

Cyrtodactylus tiomanensis Das and Lim, 2000
(Fig. 18)

Localities. - Tekek-Juara trail; Gunung Kajang at 400 m and 750 m (Lim and Lim, 1999).

New localities. - On 12 March, 2001, several specimens were observed on large boulders within and around Gua Tengkuk Air on Gunung Kajang at 845 m. On 20-22 March, 2001, several specimens were observed (LSUPC-L7002-09) on boulders, trees, and leaf-litter at the forest's edge on the beach 1 km south of Kampung Tekek. One specimen (LSUHC 4597) was collected from Telok Monkey (ca. 20 m) on 17 July, 2002. This species ranges from coastal vegetation to high hill dipterocarp forest.

Gehyra mutilata Wiegmann, 1834

Localities. - Kampung Tekek and Kampung Mukut (Hendrickson, 1966a).

New localities. - On 16 March, 2001, a specimen (LSUPC-L6080-84) was photographed during the evening on the Tekek-Juara trail at approximately 200 m. This species occurs in lowland dipterocarp forest and in disturbed habitat.

Gekko monarchus Duméril and Bibron, 1836

Localities. -Sungai Keliling (Hendrickson, 1966a).

New localities. - On 22 March, 2001, specimens (LSUPC-L7044-45) were photographed from the Tekek-Juara trail, on boulders, trees or short vegetation from 50-100 m. On 23 March, 2001, specimens (LSUPC-L7046-49) were photographed on rocks from the boulder caves on the beach 1 km south of Kampung Tekek. This species occurs in coastal vegetation and lowland dipterocarp forest.

Hemidactylus frenatus Duméril and Bibron, 1836

Localities. - Kampung Tekek (Hendrickson, 1966a).

New localities. - On 9 July, 2001, two specimens (LSUHC 3807-08) were collected at Telok Nipah at 5 m beneath the wood of an abandoned shack. On 22 March, 2001, a specimen was collected and released at Kampung Juara. This species occurs in coastal vegetation usually near human habitations.

Ptychozoon kuhli Stejneger, 1902

Localities. - On 16 March, 2001, a specimen (LSUPC-L7010-26) was photographed along the Tekek-Juara trail approximately 3 m above the ground on a large strangler fig at approximately 200 m. On 18 March 2001, an individual was found on the Tekek-Juara trail facing head down on a large dipterocarp tree approximately 6 m above the ground at 250 m. On 10 July, 2001, a single specimen (LSUHC 3835) was found on the Tekek-Juara trail on a large metal pole approximately 3 m above the ground at 142 m. On 16 July, 2001, a specimen was sighted in a coconut palm grove in Kampung Tekek at the base of the Tekek-Juara trail at 80 m. One specimen (LSUHC 5042) was collected from 20 m above ground level on the side of a tree along the Sungai Mentawak at 195 m on 11 August, 2002. These specimens confirm this species' presence on Pulau Tioman, first reported as an unconfirmed sighting by Grismer et al. (2002a). This species ranges from coastal vegetation to lowland dipterocarp forest.

Family: Scincidae

Dasia olivacea Gray, 1839

Localities. - Kampung Tekek; Kampung Paya; Sungai Asah (Hendrickson, 1966a).

New localities. - On 16 March, 2001, a specimen was observed on the Tekek-Juara trail at 200 m in elevation in primary forest. Another was seen on a large dipterocarp tree approximately 2.5 m above the ground at 80 m. On 10 July, 2001, an individual (LSUHC 3863) was collected from Kampung Mukut at 5 m. On 12 July, 2001, a sighting of a *D. olivacea* was recorded at Kampung Salang at 10 m. This species occurs from coastal vegetation to low hill dipterocarp forest.

Emoia atrocostata Lesson, 1830

Localities. - On 11 July, 2001, an individual was sighted at Kampung Salang at 10 m on a wooden bridge near the coast. On the same day a specimen was collected from intertidal rocks on neighboring Pulau Tulai (Grismer et al., 2001b). This species occurs in the mangroves and along rocky shorelines (see Hendrickson, 1966a) but remains unconfirmed for Pulau Tioman.

Eutropis multifasciata Kuhl, 1820

Localities. - Sedagong; Sungai Pasal; Tekek-Juara trail; and Kampung Paya (Lim and Lim, 1999).

New localities. - On 11 July, 2001, several specimens were sighted at Telok Dungun and Telok Dalam (10-35 m). On 12 July, 2001, specimens were observed

from Kampung Salang (10 m) and from rock cracks in the waterfall in the Sungai Raya at 80 m. One individual observed at the waterfall jumped off a rocky face into the water approximately 2 m below to escape. Many other specimens were observed along the Sungai Mentawak on 19-22 July, 2002. Juveniles were found on rocks within the stream and would jump into the water to escape. Some would dive below the surface and cling to the edge of rocks for several minutes. Many others were observed along the Gunung Kajang trail from 195-245 m in elevation. This species ranges from coastal vegetation to low hill dipterocarp forest.

Larutia seribuatensis Grismer, Leong, and Yaakob, 2003

Localities. - On 20 August, 2002, an individual (LSUPC-L182) was observed abroad on the forest floor in high hill dipterocarp forest at ca. 400 m immediately following a rain shower. This species is also known from coastal vegetation on Pulau Tulai (Grismer et al., 2003). This species ranges from coastal vegetation to high hill dipterocarp forest. It is currently being described as a new species endemic to Pulau Tulai and Pula Tioman (Grismer et al., 2003).

Lipinia vittigera Boulenger, 1894
(Fig. 19)

Localities. - Unconfirmed sighting at Kampung Asah (Lim and Lim, 1999).

New localities. - From 10-16 July, 2001, specimens were sighted at Sungai Raya (40 m), Tekek-Juara trail (210 m), the base of the Tekek-Juara trail (45 m; a juvenile with a bright orange tail), Telok Nipah (25 m), and Telok Dungun (30 m). One specimen (ZRC 2.5151) was collected in primary forest at Kampung Salang at 40 m. One specimen was cited on a tree at the base of Gunung Kajang at 291 m on 24 March, 2002. All were observed foraging on the sides of large trees 3-5 m above the ground. A hatchling (LSUHC 4814) was collected in flotsam and coral at the water's edge in Telok Monkey. These specimens confirm this species' presence on Pulau Tioman. This species ranges from coastal vegetation to low hill dipterocarp forest.

Lygosoma bowringii Günther, 1864

Localities. - On 15 March, 2001, a specimen was collected beneath a trash can in Kampung Tekek, photographed (LSUPC-L6058-66), and released. On 18 March, 2001, a specimen was observed at Kampung Juara at 5 m. On 8 July, 2001, a specimen was collected from the Tekek-Juara trail at 140 m. On 9 July, 2001, a specimen was sighted in Kampung Paya at sea level. This species ranges from coastal vegetation to lowland dipterocarp forest.

Sphenomorphus scotophilus Boulenger, 1900

Localities. - Gunung Kajang at 845 m and the Tekek-Juara trail (Lim and Lim, 1999).

New localities. - On 19 March, 2001, two specimens (LSUPC-L3286-87) were observed and photographed from the summit of Gunung Kajang at 1035 m and at Gua Tengkuk Air at 845 m. On 9 July, 2001, a specimen (LSUHC 3806) was collected at Sungai Benuang at 20 m. On 9 July, 2001, a specimen (ZRC 2.5135) was collected from the rocks in the Sungai Raya at 45 m. Several were seen on rocks along the trail south of Salang on 13 July, 2001. Additional specimens were collected from Telok Nipah (9 July, 2001; LSUHC 3806), Mukut (9 July, 2001; LSUHC 3821), and Telok Monkey (17 July, 2001; LSUHC 4595 between 10 m and 20 m). This species ranges from coastal vegetation to ridge forest.

Sphenomorphus sp.
(Fig. 20)

New localities. - On 22 March, 2002, a specimen (LSUHC 4429) of a new species of *Sphenomorphus* was collected along the Gunung Kajang Trail at 510 m in elevation. On 8 August, 2002, a hatchling of the same species (LSUHC 5031) was collected on the summit of Gunug Kajang at 1035 m. Many other specimens were observed in the leaf litter of the forest floor between 300-1035 m on Gunung Kajang. This species ranges from low hill dipterocarp to ridge forest. It is currently being described (Grismer, in prep.).

Family: Varanidae

Varanus nebulosus Gray 1831

Localities. - Sedagong; Kampung Air Batang; Kampung Salang; and Kampung Tekek (Lim and Lim, 1999).

New localities. - On 18 March, 2001, several individuals were observed in Kampung Juara basking on coconut palms 1-6 m above the ground. On 17 March, 2001, a juvenile and adult were observed along the Tekek-Juara trail (100 m and 275 m). *Varanus nebulosus* were also seen at Telok Dalam, Telok Dungun, Kampung Paya, Kampung Mukut, and Telok Nipah (0-80 m). This species ranges from coastal vegetation to lowland dipterocarp forest.

Varanus salvator Laurenti, 1768

Localities. - Sedagong; Kampung Salang; Kampung Asah; Kampung Tekek (Lim and Lim, 1999).

New localities. - On 9 July, 2001, a sighting of a *Varanus salvator* approximately 1.5 m in SVL was made in Kampung Paya at 5 m. On 16 March a sighting of a specimen was recorded in Telok Nipah. On 19 March, 2002, two specimens were observed along the banks of the Sungai Mentawak at 195 m 2 km inland from the coast. This species occurs in mangroves, coastal vegetation, and lowland dipterocarp forest provided there are waterways serving as dispersal corridors.

Family: Dibamidae

Dibamus tiomanensis Diaz, Leong, Grismer and Yaakob, 2004

Localities. - Kampung Paya (Lim and Lim, 1999); Tekek-Juara trail at 80 m (Diaz et al. 2004).

New localities. - Lim and Lim (1999) reported this population as *D.* cf. *alfredi* based on the only known specimen (ZRC 2.3410). On 14 August, 2002 a specimen was found beneath a log at Air Batang at sea level. This species is found from mangrove to lowland dipterocarp forest.

Family: Typhlopidae

Ramphotyphlops albiceps Boulenger, 1898 (Fig. 21)

Localities. - On 8 July, 2001, a specimen (ZRC 2.5125) was collected from the Tekek-Juara trail, at 241 m in elevation. It was unearthed 0.3 m below the surface of the ground in rocky soil while placing pit fall traps. This constitutes a new island record. This species occurs in low hill dipterocarp forest.

Ramphotyphlops braminus Daudin, 1803

Localities. - Kampung Juara (Day, 1990).

New localities. - On 21 March, 2001, a specimen (LSUPC-S2814) was found beneath a large piece of wood in Kampung Tekek (ca. 10 m) and photographed. On 9 July, 2001, an individual (ZRC 2.5134) was collected at Kampung Paya at 5 m. This species occurs in mangrove and coastal vegetation.

Family: Pythonidae

Python reticulatus Schneider, 1801

Localities. - Kampung Tekek and north of Telok Dungun (Hendrickson, 1966a).

New localities. - On 6 August, 2001, K. P. Lim (pers. comm.) informed LLG of a specimen measuring approximately 5 m SVL he observed in Kampung Paya on 17 July, 2001. Several specimens have been observed by JLG, LLG, and TMY at Air Batang, Berjaya, Kampung Juara, and Telok Nipah from 0-15 m. This species ranges from mangrove to lowland dipterocarp forest.

Family: Colubridae

Ahaetulla prasina Boie, 1827

Localities. - Tekek-Juara trail at the Sungai Air Besar crossing (Hendrickson, 1966a).

New localities. - On 20 March, 2001, a specimen was observed and photographed (LSUPC-S2892-99) at Gua Tengkuk Air at 845 m. On 13 July, 2001, an adult specimen (LSUHC 3914) was collected in lowland forest at Telok Dungun. Two specimens (LSUHC 4687-88) were collected from the Tekek waterfall trail at ca. 100 m on 18 July, 2002. This species occurs from coastal vegetation to high hill dipterocarp forest.

Boiga drapiezii (Boie, 1827)

Localities. - Tekek-Juara trail at 213 m in elevation. One specimen (LSUPC-S3797) was collected on 14 July 2003 2 m above the ground as it was crawling down the side of a palm tree. This species represents a new record for P. Tioman.

Boiga nigriceps Günther, 1863

Localities. - Kampung Juara at 100 m (Hien et al. 2001).

New localities. - On 26 March, 2002, an adult (LSUHC 4494) was found on the Tekek-Juara trail at night at ca.175 m as it was crawling across the trail. On 16 July, 2002, and juvenile (LSUHC 4591) was found at night 2 m above the ground in a small tree at the damn on the Tekek-Juara trail at 220 m. On 18 July, 2002, an adult (LSUHC 4686) was found crawling through brush on the Tekek waterfall trail at 185 m. This species ranges from coastal vegetation to lowland dipterocarp.

Calamaria ingeri Grismer, Kaiser, and Yaakob, 2004 (Fig. 22)

Localities. - On 22 July, 2002, a specimen of *Calamaria* (LSUHC 4716) was found within a trap in the lower pitfall trap array. On 23 July, 2002, another specimen (LSUHC 4800) was found in the same trap.

These specimens resemble *C. lovii gimletti* in coloration but lack the enlarged second supralabial of all *C. lovii* and have unique combinations of characters that set them apart from all other *Calamaria* (Inger and Marx, 1965). This population was described as *C. ingeri* (Grismer et al.,2004a). This species is found in lowland dipterocarp forest.

Chrysopelea pelias Linnaeus, 1758
(Fig. 23)

Localities. - Kampung Juara (Day, 1990).

New localities. - On 19 March, 2001, a specimen (LSUPC-S2793-2801) was observed and photographed on a large dipterocarp approximately 4 m above the ground on the Tekek-Juara trail at 195 m. We collected this snake two hours after we had collected a *Ptychzoon kuhli* from the same tree. The snake was facing head down and rapidly tongue flicking the spot where we previously collected the *P. kuhli*. We suspect it may have been scent trailing the gecko. On 11 July 2001, a specimen (ZRC 2.5145) was collected from the Tekek-Juara trail at 140 m crawling across a large boulder. This species occurs in lowland dipterocarp forest.

Dendrelaphis cyanochloris Wall, 1921

Localities. - Tekek-Juara trail and Kampung Juara (Hien et al., 2001).

New localities. - On 17 July 2001, one specimen (LSUHC 4611) was found at night sleeping in brush along the Tekek waterfall trail at 100 m. This species occurs in lowland dipterocarp forest.

Dendrelaphis pictus Gmelin, 1789

Localities. - Tekek-Juara trail (Grismer et al., 2002a).

New localities. - On 6 August 2001, K. P. Lim (pers. com., 2001) informed LLG of an observation of *D. pictus* in Kampung Juara on 21 July 2001. This species ranges from coastal vegetation to low hill dipterocarp forest.

Dendrelaphis striatus Cohn, 1906
(Fig. 24)

Localities. - Kampung Juara (Wood et al., 2003).

New localities. - On 21 July, 2001, one specimen (LSUHC 4792) was observed sleeping 2 m above ground level on a trail in Telok Monkey at 80 m. This species is found in coastal and lowland dipterocarp forest and constitutes a new record for this island.

Dryocalamus subannulatus Duméril, Bibron and Duméril, 1854

Localities. - On beach 1 km south of Kampung Tekek (Grismer et al., 2002a).

New localities. - On 14 August, 2002, one specimen (LSUHC 5051) was observed at night crawling through the branches of a tree 2 m above ground level at the bottom of the Tekek-Juara trail near the Mosque at 80 m. This species is found in coastal and lowland dipterocarp forest.

Elaphe flavolineata Schlegel, 1837

Localities. - Kampung Tekek (Wood et al. 2004)

New localities. - On xx March, 2003, one juvenile specimen (LSUHC- S3752) was found dead on the road in Kampung Tekek at 10 m in elevation. This species is found in coastal vegetation.

Elaphe taeniura Cope, 1861

Localities. - 100 m behind last house at Kampung Juara (Hien et al., 2001).

New localities. - On 19 July, 2002, one specimen (LSUHC 4675) was observed 2 m above ground level crawling on the top of a large boulder on a trail in Telok Monkey at 40 m immediately following an afternoon rainshower. This species is found in coastal and lowland dipterocarp forest.

Enhydris plumbea Boie, 1827

Localities. - Sungai Raya (Lim and Lim, 1999).

New localities. - On 9 November, 1997, two specimens (at PERHILITAN uncatalogued) were collected from the Sungai Besar in Kampung Tekek. On 9 July, 2001, a specimen (LSUHC 3817) was collected from beneath a log at Kampung Paya at sea level. This species occurs in mangroves and coastal vegetation.

Fordonia leucobalia Schlegel, 1837
(Fig. 25)

Localities. - On 15 July, 2001, a specimen (LSUPC-S3253) was collected from the drainage canals at Persona Island Resort in Kampung Tekek at 5 m and is currently maintained as a living specimen at the Raffles Museum of Biodiversity Research at the National University of Singapore. This constitutes a new island record. This species occurs in the mangroves.

Gongylosoma mukutense Grismer, Das, Leong, 2003
(Fig. 26)

Localities. - On 10 July, 2001, a specimen (ZRC 2.5141) was found at 20 m in coastal vegetation on the trail that leads from Kampung Mukut to Sungai Raya. The specimen was being eaten by a juvenile *Ptyas carinatus*. An additional specimen (LSUHC 4680) was collected from 190 m in elevation along the Tekek-Juara trail on 16 July, 2002. This species occurs in coastal vegetation and lowland dipterocarp forest.

Gonyosoma oxycephalum Boie, 1827
(Fig. 27)

Localities. - A sight record from Nipah was reported by Day (1990).

New localities. - A specimen was found resting on a branch 10 m above the surface of a small river in Kampung Juara. It was collected and photographed by Pauli Hien. A photo of that specimen is deposited at La Sierra University (LSUPC-S3633). This specimen constitutes a new island record. This species occurs in coastal forest.

Lepturophis albofuscus Duméril, Bibron and Duméril, 1854

Localities. - Sungai Nipah (Day, 1990).

New localities. - Two specimens (LSUHC 4588-89) were collected at night along the Tekek-Juara trail at 180 m and 220 m, respectively, on 16 July, 2002. An additional juvenile specimen (ZRC 2.5144) with a black and white banding pattern was collected from the Tekek-Juara trail at 200 m on 11 July, 2001. An additional specimen (LSUHC 4411) was collected along the Sungai Mentawak at 195 m on 16 July, 2002. This species occurs in lowland dipterocarp forest.

Liopeltis tricolor Schlegel, 1837

Localities. - Top of Tekek-Juara trail at 245 m (Hendrickson, 1966a).

New localities. - A single adult (LSUHC 5037) was collected during the day along the Gunung Kajang trail at 618 m while resting on a small branch 2 m above ground level. This species ranges from lowland dipterocarp to high hill dipterocarp forest.

Oligodon purpurascens Schlegel, 1837
(Fig. 28)

Localities. - Ulu Lalang and the Tekek-Juara trail (Hendrickson, 1966a; Day, 1990).

New localities. - On 9 July, 2001, a shed skin (LSUHC 3988) with a pattern matching that of *Oligodon purpurascens* was found at Telok Dungun within a rotting log at 15 m. On 11 August, 2002, an adult was found crawling across the forest floor during the day at 320 m on the Gunung Kajang trail. The Pulau Tioman population is unlike all others in that the snakes are bright red-orange in dorsal color and have smooth as opposed to irregular dorsal band margins. This population is under further investigation. This species ranges from lowland dipterocarp forest to high hill dipterocarp forest.

Oligodon booliati Leong and Grismer, 2004

Localities. - Ulu Lalang (Hendrickson1966a).

New localities. - On 16 July, 2001 a specimen (ZRC 2.5153) was collected from the Tekek-Juara trail at approximately 150 m in elevation. It differs from all other *Oligodon* by its bright red coloration and extremely faint banding pattern. Its scale counts fall within the range of those of *O. signatus* (Leong and Grismer, 2004). Hendrickson (1966a) reported *O. signatus* at Ulu Lalang in high hill dipterocarp forest. Upon examination of that specimen (BPBM 13933) we find that it conforms to the new species (ZRC 2.5153) reported above. This species ranges from lowland dipterocarp forest to high hill dipterocarp forest.

Pareas vertebralis Boulenger, 1900

Localities. - Gua Tengkok Air at 810 m (Youmans et al., 2003).

New localities. - On xx March, 2003 an adult specimen (LSUPC S3696-4000) was observed crawling throught he lower branches of a small tree approximately 1.5 m above the ground. This species is known only from high hill dipterocarp forest.

Psammodynastes pulvurulentus Boie, 1827

Localities. - Summit of Gunung Kajang at 1035 m (Day, 1990).

New localities. - On 17 July, 2002 a juvenile specimen (LSUHC 4684) was collected along the Tekek-Juara trail while sleeping on a leaf at 230 m. Another specimen was collected and photographed (LSUPC-S3631) from Air Batang near sea level by Johan van Rooijen. This species ranges from coastal vegetation to ridge forest.

Ptyas carinatus Günther, 1858

Localities. - Tekek-Juara trail (Grismer et al., 2002a).

New localities. - On 3 November, 2000, a large adult (LSUPC-S2774-80) was photographed on the Tekek-Juara trail at 240 m in elevation. On 10 July 2001, a juvenile (ZRC 2.5142) was found on the trail that leads from Kampung Mukut to the Sungai Raya at 20 m. The latter specimen was found eating a *Gongylosoma mukutense.* On 20 July, 2002, an adult was found crawling during the day on the Tekek waterfall trail at 100 m. This species ranges from coastal vegetation to lowland dipterocarp forest.

Rhabdophis chrysargos Schlegel, 1837
(Fig. 29)

Localities. - Forest behing Kampung Juara (Henrickson, 1966a).

New localities. - Hien et al. (2001) report this species from the Sungai Mentawak at 150 m, at the mouth of the Sungai Mentawak at sea level, and at Tanjung Pisang Kera and Tanjung Batu Pulau at sea level. We found a specimen (LSUHC 4791) at 80 m on the Tekek-Juara trail near the Mosque. Hien et al. (2001) report this population as *Amphiesma* sp. All specimens we examined are within the variation reported for *Rhabdophis chrysargos* except for coloration. Specimens from the Pulau Tioman differ from others in that adults are red anteriorly and juveniles are red-orange throughout. Also, the white nuchal line is faint to absent. This species occurs from mangroves to lowland dipterocarp forest.

Sibynophis melanocephalus Gray, 1834
(Fig. 30)

Localities. - On 18 July 2002, an adult (LSUHC 4683) was found crawling through the grass in Kampung Juara (Grismer et al., 2003). During capture, it voluntarily broke off two sections of its tail in defense. This specimen constitutes a new record for Pulau Tioman. This species occurs in coastal vegetation.

Family Elapidae

Calliophis intestinalis Laurenti, 1768

Localities. - Telok Nipah and the Tekek-Juara trail (Day, 1990).

New localities. - On 19 March, 2001, a specimen (LSUPC-S1038-40) was photographed on the trail to Gunung Kajang at approximately 100 m in elevation near the Sungai Mentawak. On 19 July, 2002, one specimen (LSUHC 4617) was taken from a pitfall trap from the upper array at 241 m. On 10 August, 2002, a specimen (LSUHC 5047) was collected crawling through the leaf litter at Gua Tenguk Air at 845 m on Gunug Kajang. This species occurs from lowland dipterocarp to high hill dipterocarp forest.

Ophiophagus hannah Cantor, 1836

New localities. - A large adult (ca. 3.5 m) was photographed by Johan van Roojen in March, 2002 at Air Batang at sea level (Van Rooijen and Van Rooijen, 2002). On Pulau Tioman this species is known only from coastal vegetation but local people say it occurs throughout the island (Hendrickson, 1966a). This species occurs in mangrove and coastal vegetation.

Family: Viperidae

Trimeresurus sp.
(Fig. 31)

Localities. - Gunung Kajang at 400 m (Lim and Lim, 1999); Gua Tenguk Air at 845 m (Day, 1990).

New localities. - On the evening 21 July, 2002, a male was collected while sitting 7 m above ground level on the end of a branch along the Tekek-Juara trail at 210 m. Lim and Lim (1999) referred to this species as *Trimeresurus* cf. *popeiorum*. Its specific status is currently being investigated. This species ranges from lowland to high hill dipterocarp forest.

Results and Discussion

The amphibians and reptiles of Pulau Tioman have varying patterns of distribution (Table 1). Some species (i.e., *Cyrtodactylus tiomanensis* and *Psammodynastes pulverulentus*) range throughout many different vegetation zones from coastal vegetation to ridge forest whereas others, such as *Philautus petersi*, *Draco haematopogon* and *Pareas vertebralis* are restricted to only high elevations in high hill dipterocarp and/or ridge forest (Table 1). The majority of the species, however, are found in lowland dipterocarp forest (Table 1). This region supports 74% of the amphibians, 76% of the lizards, and 74% of snakes, totaling 74% of the island's species composition. The high species diversity in this vegetative zone is due largely to its varied habitat and microhabitat composition. Here, the terrain is characterized by many large boulder outcrops and fast flowing, boulder-strewn streams. The crevices, exfoliations, and shaded refugia offered by the boulders, along with the additional microhabitats these features provide along a water course, add

greatly to the microhabitat diversity of this forest. Such microhabitat diversity allows many species to specialize into narrow environmental zones. In fact, species which range throughout all the vegetative zones (i.e., *Sphenomorphus scotophilus* and *Cyrtodactylus tiomanensis*) do so because of their association with the microhabitats offered by boulders. There are more restricted species such as *Ansonia tiomanica* which occur only in habitats with large boulders in the vicinity of water at elevations above 220 m. Whereas others (i.e., *Rana hosii*, *Ichthyophis* sp., *Dogania subplana*, *Gonocephalus grandis*) are confined to riparian habitats.

The species composition of the distribution patterns will undoubtedly change with the acquisition of additional specimens. Many of the species reported from Pulau Tioman are known from a limited number of individuals and thus, appear to exist in a limited range of habitats. These species range throughout a far greater number of habitats on peninsular Malaysia and so it is likely they do so as well on Pulau Tioman. However, even with the acquisition of new material the generality of the observed trends in habitat use are not likely to change significantly.

There are two sightings of unconfirmed species on Pulau Tioman listed in an unpublished report by Day (1990). Day's sightings range from specimens he actually observed to second hand reports he received from locals, vacationers, and friends. Species he personally observed (i.e., *Chrysopelea paradisi*; see Lim and Lim, 1990 for discussion) are considered as potentially present. The others, *Leiolepis belliana* and *Elaphe porphyracea* are not considered noteworthy herein. Day (1990) also reported *Rana doriae* from a small tributary of the Sungai Mentawak at 290 m. Examination of these specimens (uncatalogued in the British Museum of Natural History) show them to be *Limnonectes blythii*. Hien et al. (2001) report that the *Lycodon effraenis* reported by Manthey and Grossman (1997) was a juvenile *Lepturophis albofuscus*.

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Pareas stanleyi - A Record New to Sichuan, China and a Key to the Chinese Species

PENG GUO[1] AND ERMI ZHAO[2]

[1]*College of Life Sciences, Sichuan University, Chengdu, Sichuan, China 610041*
[2]*Chengdu Institute of Biology, Chinese Academy of Sciences Chengdu, Sichuan Province, China 610041*

Abstract. - A specimen of the Fujian slug-eating snake, *Pareas stanleyi*, was collected in Sichuan Province, China for the first time. We provide a key to the Chinese species of *Pareas.*

Key words. - Serpentes, Colubridae, *Pareas*, China, Sichuan.

An adult male of the Fujian slug-eating snake, *Pareas stanleyi* (Boulenger, 1914) was captured from Muchansi, Liujiang Town, Hongya County, Southwestern Sichuan Province, China at noon on 02 June, 2003 (Fig. 1). This species was first described based on one male specimen from N. W. Fokien (=Fujian Province). It was successively found in Zhejiang (Longquan), Jiangxi (Mt. Jinggangshan), Guizhou (Leishan), and also Fujian (Chongan, Nanjing, Pucheng, Shaowu). All the localities are situated within 108° 10' N, 119° 10' E and 26° 20' N, 28° 10' N. The geographic position of Liujiang Town is between 29° 44' N and 103° 13' E . The discovery of *Pareas stanleyi* from Liujiang Town extends its range about 5 degrees westward and about 1.5 degrees northward. The distribution pattern of *Pareas stanleyi* is Southern China.

SCU No. 20030049

An adult male. Head distinct from the neck, snout blunt, body somewhat compressed. Rostral high, visible from above of the head; internasals shorter than prefrontals; no preoculars; loreals large, its posterior end entering the eye; prefrontals extending laterally to the sides of the head, and touching the eye at its anterior upper corner; supraoculars small; postoculars narrower and in contact with the long narrower crescent subocular, which completely encircling the posterior and inferior border of the eye; two anterior temporals, three posterior temporals; upper labials seven, excluded from orbit; mental very small; lower labials eight, anterior three or four in contact with the anterior chin-shield; the latter three pairs, no mental groove. Dorsal scales in fifteen rows throughout, three median rows feebly keeled at the neck region, seven median rows feebly keeled at the midbody, all but the outer one row keeled before the vent, vertebral row not enlarged; ventrals 153; anal entire; subcaudals in pairs, 54/54+1. The coloration of this specimen is identical with the original description by G. A. Boulenger (1914). The total length of the male Hongya specimen is 630.5 mm with a tail length of 110.5 mm. The tail is about 17.5% of the total length.

Figure 1. *Pareas stanleyi* from Sichuan Province, China.

Twenty species belong to the genus *Pareas* Wagler, 1830 (Welch, 1988). It ranges over East Asia, Southeastern Asia, and South Asia (Bangladesh, Burma, China, India [Assam], Indonesia, Japan, Kampuchea, Laos, Malaysia, Sikkim, Thailand, and Vietnam). In China, nine species are recognized (Zhao et al., 1998). The authors of this paper believe that *Pareas macularius* Theobald, 1868 is a synonym of *P. margaritophorus* (Jan, 1866), *P. komaii* (Maki, 1931) is a synonym of *P. formosensis* (VanDenburgh, 1909), and *P. chinensis* (Barbour, 1912) may be a synonym of *P. hamptoni* (Boulenger, 1905). Thus, there are only seven species found in China, which may be distinguished by means of the following key:

Key to Chinese *Pareas*

1A Color purplish blue or purplish brown, with many black and white dorsal scales forming many short transverse bands .....*Pareas margaritophorus*
1B Color dark or light brown, many dorsal scales with small black spots forming transverse line or reticulation 2

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2A No prefrontal.....*Pareas carinatus*
2B With prefrontal and entering the eye.....3

3A No preocular, loreal entering the eye.....4
3B Preocular present, loreal not entering the eye (or only its tip entering the eye) 6

4A Dorsal scales smooth.....5
4B Dorsal scales keeled but the outer row smooth; back of head with big black blotch.....*Pareas stanleyi*

5A Vertebral enlarged; the fourth upper labial entering the eye; ventrals more than 190; subcaudals more than 72; a black "X"-shaped mark behind the parietals.....*Pareas monticola*
5B Vertebral not enlarged; the fourth upper labial not entering the eye; ventrals less than 190; subcaudals less than 77 .....*Pareas boulengeri*

6A The second upper labial touching or not touching the crescent subocular, found only in Taiwan Province.....*Pareas formosensis*
6B The second upper labial not touching the crescent subocular, found in mainland .....*Pareas hamptoni*

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Intraspecific and Interspecific Genome Size Variation in Hynobiid Salamanders of Russia and Kazakhstan: Determination by Flow Cytometry

Spartak N. Litvinchuk[1,*], Leo J. Borkin[2] and Jury M. Rosanov[1]

[1]*Institute of Cytology, Russian Academy of Sciences, Tikhoretsky pr. 4, St. Petersburg 194064, Russia;*
**E-mail: slitvinchuk@yahoo.com*
[2]*Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg 199034, Russia*

Abstract. - The amount of DNA per diploid nucleus in *Salamandrella keyserlingii* and *Onychodactylus fischeri* from Russia, as well as in *Ranodon sibiricus* from Kazakhstan was determined by flow cytometry. *Onychodactylus fischeri* had the highest genome size, *Ranodon sibiricus* the lowest, and *Salamandrella keyserlingii* was intermediate. Obvious geographic variation in genome size was revealed for *Salamandrella keyserlingii* and *Ranodon sibiricus*. The comparison of nuclear DNA content in eleven hynobiid species supported the genus *Onychodactylus* as a separate lineage.

Key words. - nuclear DNA content, genome size, flow cytometry, Caudata, Hynobiidae, *Onychodactylus fischeri*, *Salamandrella keyserlingii*, *Ranodon sibiricus*, Russia, Kazakhstan.

Introduction

Diploid genome size, measured in picograms (pg; 1 pg = 10^{-12} g) of DNA per nucleus, varies widely in vertebrates. Living amphibians represent the largest range of genome size variability among terrestrial vertebrates, with a minimum of 1.7 pg in male frogs of *Eleutherodactylus shrevei* (Schmid et al., 2002) and maximum of 241 pg in *Necturus lewisi* (Olmo, 1973). Some extinct amphibians may have had maximum DNA contents greater (approximately 300 pg) than the maximum known in living forms (Thoson and Muraszko, 1978).

Various methods are used for the measuring of genome size in amphibians (for example, biochemical analysis, Feulgen densitometry, static cell fluorometry, ultraviolet microscopy, etc.). However, modern studies are based on a comparatively new and very precise method of flow DNA cytometry. As a rule, standard errors of this method (peak mean ratios) are less than 0.5% (Rosanov and Vinogradov, 1998). Among approximately 415 amphibian species examined, nuclear DNA contents were studied by flow cytometry in about 143 species only (Gregory, 2001a).

Among some specific applications, DNA flow cytometry has been used to examine ploidy levels (Borkin et al., 1986, 1996, 2001a; Vinogradov et al., 1990; Sharbel et al., 1997; Litvinchuk et al., 1998, 2001), to identify morphologically similar species (Sharbel et al., 1995; MacCulloch et al., 1996; Litvinchuk et al., 1997, 1999; Murphy et al., 1997; Borkin et al., 2001b, 2003; Khalturin et al., 2003), and to search for hybrid individuals (Borkin et al., 1987, 2002; Litvinchuk et al., 2003). Many authors have noted a relationship between genome size and some biological parameters, such as cellular and nuclear sizes, replication time, cell-cycle length, cell division rate, metabolic rate, longevity, morphological complexity in the brain, etc. (Van't Hoff and Sparrow, 1963; Goin et al., 1968; Olmo and Morescalchi, 1975; Bachmann and Nishioka, 1978; Sessions and Larson, 1987; Shakhbazov and Gapchenko, 1990; Licht and Lowcock, 1991; Nevo and Beiles, 1991; Roth et al., 1994; Vinogradov, 1999; Gregory, 2001b, 2001c; Griffith et al., 2003). However, an adaptive value of genome size is most clearly shown in its relationship with the timing of embryonic development in amphibians (Bachmann, 1972; Oeldorf et al., 1978; Horner and Macgregor, 1983; Pagel and Jonstone, 1992; Jockusch, 1997; Chipman et al., 2001; Gregory, 2002, 2003).

This research is focused on salamanders of the family Hynobiidae, which consists of approximately 42 species. Among modern amphibians, hynobiids are recognized to be one of the primitive urodelans (e.g., Duellman and Trueb, 1986; Larson and Dimmick, 1993). Hynobiids inhabit various mountain regions of Palaearctic Asia, where they have quite restricted ranges. The territory of Russia and Kazakhstan are only inhabited by three hynobiid species. Other family members, such as the Siberian Salamander (*Salamandrella keyserlingii*), is widely distributed from Northeastern European Russia to the Kamchatka Peninsula. The Ussuri Clawed Salamander (*Onychodactylus fischeri*) can be found in the southern part of Russian Far East and in the Korean Peninsula. The Semirechensk salamander (*Ranodon sibiricus*) inhabits the Dzhungarsky Alatau

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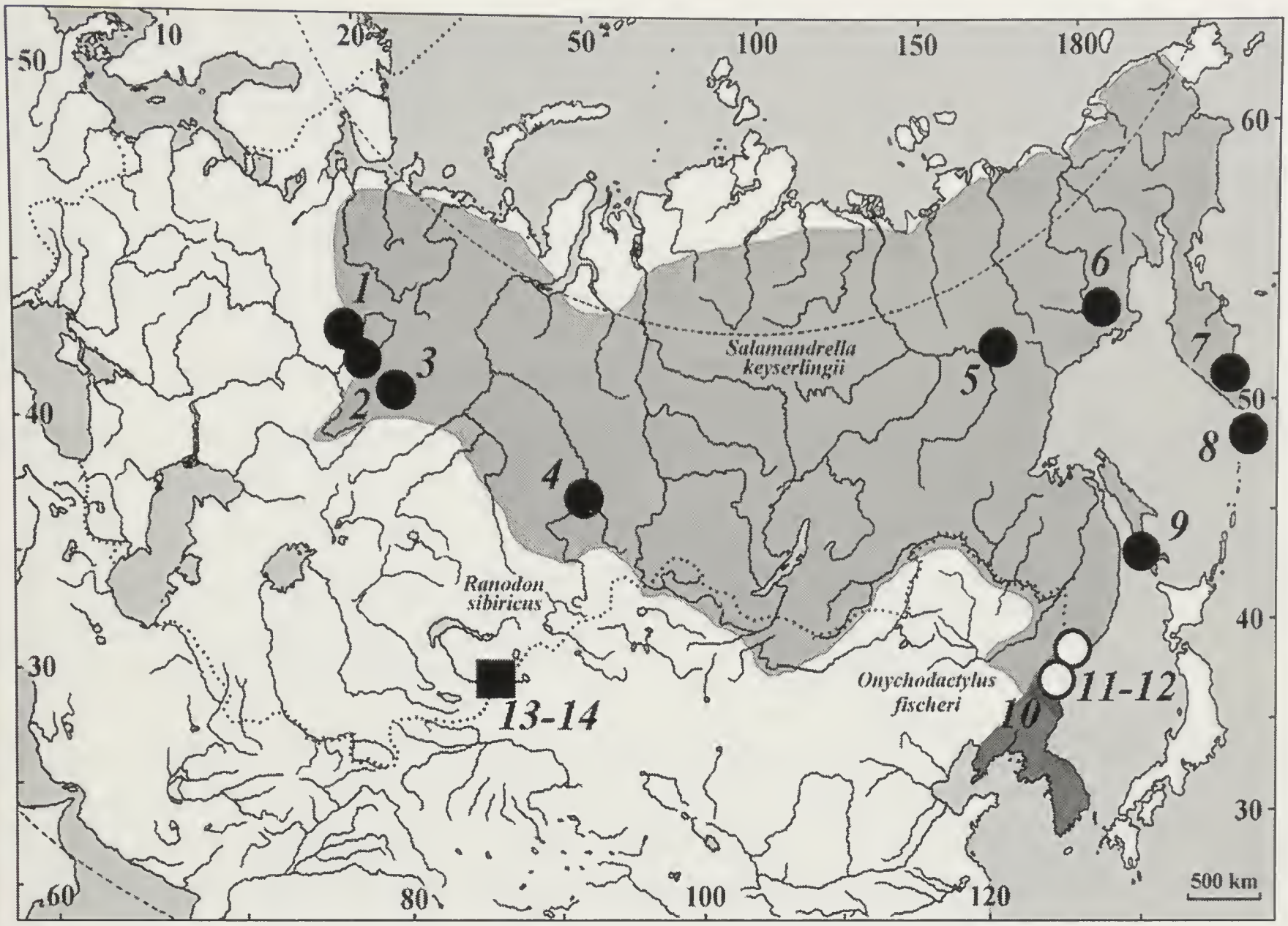

Figure 1. Distribution of *Salamandrella keyserlingii* (grayish area), *Ranodon sibiricus* (dark square), and *Onychodactylus fischeri* (dark-grayish area), with localities studied (locality number as in Table 1). Dark circles designate the "Euro-Siberian" type of *Salamandrella keyserlingii*, white ones - "Primorsky" type.

Mountains in southeastern Kazakhstan and adjacent China. The last two species are included in the Russian and Kazakhstan Red Data Books, respectively. *Ranodon sibiricus* is also included in the IUCN Red List of Threatened Animals under the category "vulnerable" (Borkin, 1998; Kuzmin, 1999). The goal of present paper is to evaluate the intra- and interspecific genome size variation in three hynobiid species of Russia and Kazakhstan, with flow cytometry.

Materials and methods

Eighty-eight metamorphosed specimens from 13 populations of three species distributed in Russia and Kazakhstan were used in this study of genome size variation. Blood was taken from the clipped tail tip. The samples of *Salamandrella keyserlingii* and *Onychodactylus fischeri* studied are kept at the collections of the Department of Herpetology, Zoological Institute, Russian Academy of Sciences. All specimens of *Ranodon sibiricus* were obtained from the Almaty Zoo (Kazakhstan), and after preparation of blood samples, the live salamanders were sent to the Moscow Zoo.

Peripheral blood cells of specimens of the Ribbed Newt, *Pleurodeles waltl*, received from Prof. J. C. Lacroix (Université Paris VI, Paris, France) were used as a reference standard. Details of the technique have been published previously (Vinogradov et al., 1990; Rosanov and Vinogradov, 1998; Borkin et al., 2001). The relative genome size differences (RD) were calculated with use of formula: RD=(m1-m2)/(m1+m2) × 200%, where m1 and m2 are the sample means.

Results

The genome size variation in three hynobiid species varied between 54.5 and 109.0 pg (Table 1). The lowest nuclear DNA content was recorded in *Ranodon sibiricus* (in average 55.4 pg), whereas the highest was in *Onychodactylus fischeri* (107.7 pg). *Salamandrella keyserlingii* was intermediate in size (66.4 pg).

Differences between populations were studied in two species, represented by more than one sample. In *S. keyserlingii*, ten samples were allocated to two main, distinct groups with different genome sizes (Table 1 and Fig. 1). The geographic distribution of these two groups

Table 1. Locality of origin ("Lat" is latitude, and "Lon" is longitude), sample size, genome size (in picograms; SD is standard deviation) with the coefficient of variation (CV; in percents) for 13 populations of three hynobiid species.

Province/Region	Locality	Lat	Lon	n	Mean	SD	Range	CV
***Salamandrella keyserlingii* (Russia)**								
The "Euro-Siberian" group								
1 Nizhny Novgorod	Pizhma	57°52'	47°05'	5	66.7	0.2	66.5 - 66.9	0.3
2 Udmurtia	Chur	57°06'	52°59'	10	67.5	0.4	66.7 - 68.1	0.6
3 Ekaterinburg	Ekaterinburg	56°51'	60°43'	15	66.6	0.5	65.5 - 67.7	0.8
4 Tomsk	Tomsk	56°31'	84°58'	11	66.6	0.6	66.0 - 68.0	0.9
5 Yakutia	Khandyga	62°39'	135°33'	2	67.8		67.5 - 68.0	
6 Kamchatka	Petropavlovsk	53°02'	158°38'	1	66.8			
7 Kurile Islands	Paramushir Island	50°41'	156°07'	2	67.1		66.8 - 67.4	
8 Sakhalin Island	Aniva	46°43'	142°31'	2	66.5		66.3 - 66.6	
TOTAL (for the group)				48	66.9	0.6	65.5 - 68.1	0.9
The "Primorsky" type								
9 Primorsky	Kedrovaya Pad' Reserve	43°07'	131°32'	11	64.8	0.3	64.4 - 65.2	0.4
10 Primorsky	Ussuriysk Reserve	43°38'	132°09'	2	64.8		64.7 - 64.8	
	TOTAL (for the group)			13	64.8	0.2	64.4 - 65.2	0.4
	TOTAL (for the species)			61	66.4	1.0	64.4 - 68.1	1.5
Onychodactylus fischeri (Russia)								
11 Primorsky	Ussuriysk Reserve	43°38'	132°09'	7	107.7	0.7	106.7 - 109.0	0.7
***Ranodon sibiricus* (Kazakhstan)**								
12 Taldy-Kurgan	Oy-Saz River	44°51'	79°02'	10	54.8	0.2	54.5 - 55.1	0.3
13 Taldy-Kurgan	Borokhudzir River	44°30'	79°28'	10	56.0	0.6	55.1 - 56.7	1.0
	TOTAL			20	55.4	0.7	54.5 - 56.7	1.3

Table 2. The genome size (GS; in picograms) of hynobiids, referred by some authors.

Species	Locality	GS	Reference
Hynobius (Hynobius) dunni	unknown	33.76[2]	Olmo, 1973
H. (H.) nebulosus	unknown	38.40[2]	Olmo, 1973
H. (H.) tsuensis	unknown	32.96[2]	Olmo, 1973
H. (Satobius) retardatus	unknown	38.31[2]	Olmo, 1973
H. (Pseudosalamandra) naevis	unknown	40.90[2]	Olmo, 1973
Onychodactylus fischeri	Ussuriysk Reserve	45.5[2]	Mazin, 1978
	-//-	95.08[1]	Vinogradov, 1998
	-//-	107.7[1]	Present paper
O. japonicus	unknown	102-106[2]	Olmo, 1983
Paradactylodon gorganensis	Shirabad cave	34.77[1]	Stöck, 1999
P. mustersi	unknown	43.3[2]	Morescalchi et al., 1979
Ranodon sibiricus	Tekeli	50.7[2]	Morescalchi et al., 1979
	-//-	45.591[1]	Vinogradov, 1998
	2 localities	55.4[1]	Present paper
Salamandrella keyserlingii	Yakutia	42.5[2]	Mazin, 1978
	Ekaterinburg	42.3[2]	Morescalchi et al., 1979
	unknown	38[2]	Grafodatsky and Grigoriev, 1982
	Ekaterinburg	33.2[3]	Vladychenskaya et al., 1988
	-//-	55.481[1]	Vinogradov, 1998
	10 localities	66.41[1]	Present paper

[1]Flow cytometry; [2]Feulgen's densitometry; [3]Kinetics reassociation.

Table 3. Genome size (2C), range of egg diameters (mm), and time of embryonic ("Embr.") and larval ("Larv.") development (days) in some hynobiids.

Taxon	2C	Reference	Egg	Embr.	Larvae	Reference
Hynobius dunni	33.8	Olmo, 1973	2.0	-	-	Thorn, 1969
H. nebulosus	38.4	Olmo, 1973	2.6-5.0	25-30[3]	138-274[1]	Thorn, 1969
H. tsuensis	33.0	Olmo, 1973	4.0	-	90-150[1]	Thorn, 1969
H. retardatus	38.3	Olmo, 1973	2.3-3.1	21-28[2]	80-720[2]	Sasaki, 1924; Mikamo, 1956
H. naevis	40.9	Olmo, 1973	5.0-5.3	8-41[1]	120[1]	Thorn, 1969
Onychodactylus fischeri	107.7	Present paper	5.0-8.0	360[2]	780-1500[2]	Smirina et al., 1994; Griffin and Solkin, 1995; Kuzmin, 1995
O. japonicus	104.0	Olmo, 1983	4.5-5.4	120-150[3]	~1000	Iwasawa and Kera, 1980; Hayase and Yamane, 1982
Paradactylodon gorganensis	34.8	Stöck, 1999	-	-	>360[2]	Stöck, 1999
P. mustersi	43.3	Morescalchi et al., 1979	-	-	>360[2]	Reilly, 1983
Ranodon sibiricus	55.4	Present paper	3.0-5.0	21-42[2]	230-720[2]	Lebedkina, 1964; Brushko, Narbaeva, 1988; our data
Salamandrella keyserlingii	66.4	Present paper	2.1-3.5	14[4]	78-110[1]	Ishchenko et al., 1995a,b; Berman, 1996

[1]Laboratory conditions (temperature unknown); [2]nature conditions; [3]t = 10°; [4]t = 16°.

Table 4. Genome size (2C), diploid number of chromosomes (2n) and number of uniarmed macrochromosomes (UM) in some hynobiids.

Taxon	2C	Reference	2n	UM	Reference
Hynobius dunni	33.8	Olmo, 1973	56	0	Morescalchi et al., 1979; Seto et al., 1986
H. nebulosus	38.4	Olmo, 1973	56	0-2	Seto et al., 1986; Kuro-o et al., 1987
H. tsuensis	33.0	Olmo, 1973	56	0	Seto et al., 1986
H. retardatus	38.3	Olmo, 1973	40	0	Azumi and Sasaki, 1971; Kuro-o et al., 1987
H. naevis	40.9	Olmo, 1973	58	0	Kohno et al., 1987
Onychodactylus fischeri	107.7	Present paper	78	0	Iizuka and Yazawa, 1994
O. japonicus	104.0	Olmo, 1983	78	0	Morescalchi et al., 1979; Kohno et al., 1991
Paradactylodon gorganensis	34.8	Stöck, 1999	62	0	Stöck, 1999
P. mustersi	43.3	Morescalchi et al., 1979	62	10	Morescalchi et al., 1979
Ranodon sibiricus	55.4	Present paper	66	18	Morescalchi et al., 1979
Salamandrella keyserlingii	66.4	Present paper	62	26	Kohno et al., 1991

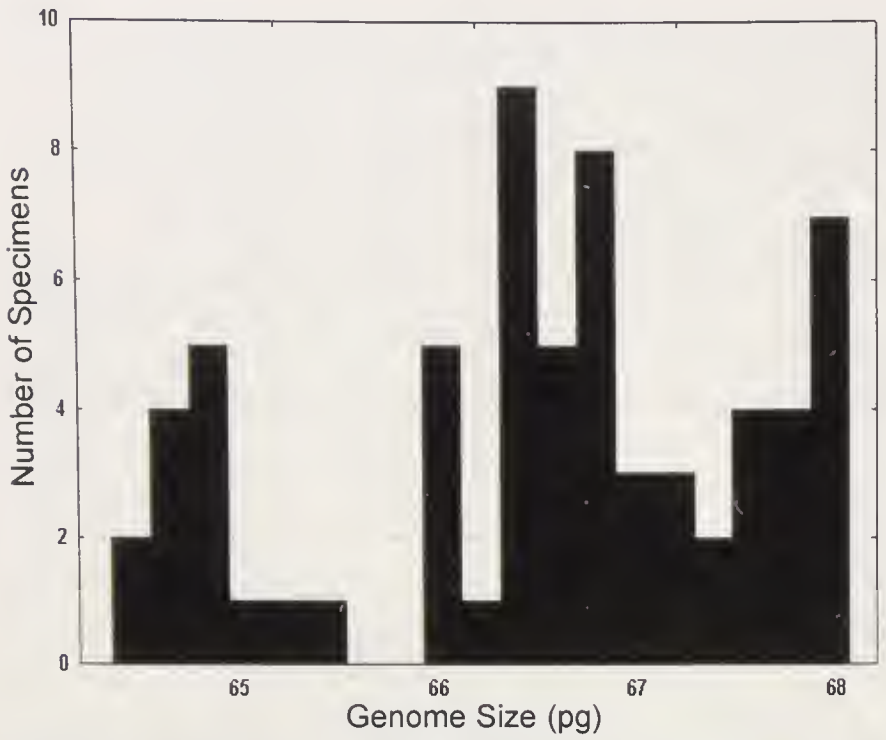

Figure 2. Genome size distribution in *Salamandrella keyserlingii*.

of samples proved to not be chaotic and the "Euro-Siberian" (8 samples) and "Primorsky" (2 samples) groups were recognized. The data ranges of the groups did not overlap, and the gap between both groups was equal to 0.3 pg (Fig. 2). The "Primorsky" samples were characterized by smaller genome size in comparison with the "Euro-Siberian" ones: 64.4-65.2 pg vs. 65.5-68.1 pg; the means were 64.8 pg vs. 66.9 pg. The differences (RD) between means were equal to 3.2%, and were observed in five separate comparisons. Therefore, these groups were shaped both by genome size and geographically.

The samples of *R. sibiricus* were taken from two semi-isolated populations from upper parts of Borokhudzir and Oy-Saz rivers. Both samples demonstrated different genome sizes (Table 1). The ranges of genome size values in these two samples slightly overlapped. The Oy-Saz sample was characterized by smaller genome size in comparison with the Borokhudzir sample: 54.5-55.1 pg vs. 55.1-56.7 pg; the means are 54.8 pg vs. 56.0 pg. The differences (RD) between means were equal to 2.2%.

The coefficient of variation (CV) ranged between 0.3% and 0.9% in *S. keyserlingii*, between 0.3% and 1.0% in *R. sibiricus*, and was equal to 0.7% in the sample of *O. fischeri* (Table 1). The overall within-species genome size variation in *S. keyserlingii* and *R. sibiricus* were quite similar (1.5% and 1.3%, respectively). Among the "Euro-Siberian" samples of *S. keyserlingii*, the CVs ranged between 0.3% (Nizhny Novgorod Province) and 0.9% (Tomsk Province), whereas it was equal to 0.4% in the "Primorsky" samples of *S. keyserlingii*.

Discussion

1) Genome size values in hynobiids: literature data

Presently, the nuclear DNA content has been determined for eleven hynobiid species. However, among them, only four species were examined through flow cytometry (Table 2). The first data collected about genome size of nine hynobiid species was obtained by Italian researchers with an application of Feulgen densitometry (Olmo, 1973, 1983; Olmo and Morescalchi, 1975; Morescalchi et al., 1979). According to these data, genome size in hynobiids ranged from 32.96 pg in *Hynobius tsuensis* to 102-106 pg in *Onychodactylus japonicus* (Table 2). According to Mazin (1978), the nuclear DNA content in two Russian species, *Onychodactylus fischeri* and *Salamandrella* ("*Hynobius*") *keyserlingii*, measured by Feulgen densitometry, were similar to each other (45.5 and 42.5 pg, respectively). Grafodatsky and Grigoriev (1982) estimated genome size of *Salamandrella keyserlingii* (38 pg), perhaps, by means of Feulgen densitometry. Vladychenskaya et al. (1988) studied kinetics of DNA reassociation; they found that the nuclear DNA content of *Salamandrella keyserlingii* was equal to 33.2 pg. Using DNA flow cytometry, Vinogradov (1998) estimated genome size values as 95.08 pg for *Onychodactylus fischeri*, 45.59 pg for *Ranodon sibiricus*, and 55.48 pg for *Salamandrella keyserlingii*. Finally, Stöck (1999) determined that genome size of *Batrachuperus gorganensis* is 34.77 pg, using DNA flow cytometry as well.

The literature values of genome size for *Onychodactylus fischeri*, *Ranodon sibiricus*, and *Salamandrella keyserlingii* expressed in absolute units vary sometimes more than two-fold (ranges are 45.5-95.1 pg, 45.6-50.7 pg, and 33.2-55.5 pg, respectively). Therefore, the comparison of data provided by various authors should be made cautiously. The contradictions may be explained by an application of different techniques (Feulgen densitometry, kinetics reassociation, and flow cytometry), dyes, and laboratory conditions (cell preparation methods, devices for measurements, types of reference cell standards, etc.). It has been shown that genome size measured with fluorochromes of different nucleotide specificity may differ markedly (e.g., Johnston et al., 1987; Birshtein et al., 1993; Vinogradov and Borkin, 1993). For instance, the determination of genome size by means of flow cytometry for cell samples of *Salamandrella keyserlingii* stained with olivomycin and Hoechst (GC- and AT-specific fluorochromes, respectively) provided 6.68 and 4.77 arbitrary units (*Rana temporaria* was taken as an internal reference; Vinogradov, 1998). To exclude the influence

of AT/GC-structure, it is necessary to use ethidium bromide or propidium iodide (Vinogradov and Borkin, 1993), which were used in our research.

To convert genome size from the relative units to picograms, it is necessary to have data about genome size of reference cells. Such data should be obtained without using stains. Unfortunately, the data available today, mentioned by various authors, do not correspond to each other. For instance, Vinogradov (1998) reported a genome size of reference standard *Mus musculus* to be 6.5 pg. Our estimations of genome size of some mammals (*Homo sapiens*, *Mus musculus*, *Rattus norvegicus*) were the closest to that mentioned by Bianchi et al. (1983). In our work, we used the genome size of males of *Mus musculus* (C57B1) as a basic reference standard with value of 6.8 pg. Other authors preferred other reference standards, which have different base-pair-specificity of some stains widely used in flow cytometry. Vinogradov and Borkin (1993) listed the AT- and GC-pair specific DNA contents (CAT and CGC) for many species of amphibians. For instance, CAT/CGC was equal to 1.42 in *Xenopus laevis* (Mazin's reference standard), and 1.00 in *Rana lessonae* (= *Rana "esculenta"*; Olmo's and Morescalchi's standard).

The estimations of Italian authors (Olmo, 1973, 1983; Morescalchi et al., 1979) and our genome size values for *Ranodon sibiricus* (50.7 and 54.5-56.7 pg, respectively) and members of genus *Onychodactylus* (102.0-106.0 and 106.7-109.0 pg, respectively) are quite similar. However, data for *Salamandrella keyserlingii* (42.3 and 64.4-68.1 pg, respectively) are in obvious discordance. The genome size of *Onychodactylus fischeri*, *Ranodon sibiricus*, and *Salamandrella keyserlingii* mentioned by Vinogradov (1998), was lower than our values, who used other stains and lower genome size estimation of basic reference standard.

Unfortunately, some authors did not supply any information about sample sizes and localities. However, some differences in genome size might be influenced by intra-population and geographic variation as well.

2) Within-species variation

Some authors discussed the levels of intraspecific variation in genome size. We recognized two kinds of such a variation; namely, the "within-population" variation and "between-population" (or geographical) variation.

A) *Within Population Variation*
Among amphibians, the greatest intrapopulational variation (CV = 7.5%, the data of Licht and Lowcock, 1991 were recalculated by us) was recorded for the Western Red-back Salamander (*Plethodon vehiculum*). However, the variation in other amphibian species was considerably lower (Licht and Lowcock, 1991; MacCulloch et al., 1996; Murphy et al., 1997; Lizana et al., 2000). The variation within populations of three hynobiid species (CVs were 0.3-1.0%, mean was 0.67 ± 0.12%) was quite similar to that in salamandrids (range is 0.1-1.7%, mean is 0.64 ± 0.03%, 99 populations studied), pelobatids, and other anurans studied in our laboratory at the same conditions (Litvinchuk et al., 1997, 1999, 2001a,b, 2003; Rosanov and Vinogradov, 1998; Borkin et al., 2001b, 2003; our data).

Sexual dimorphism in genome size has been registered in some amphibian species (Schmid et al., 2002; our data). Unfortunately, in the hynobiids examined by us, sexual differences are not expressed in external characters beyond the breeding time. Our study was based mostly on juvenile and non-breeding adult animals, and, therefore, we failed to reliably identify the sex without anatomical dissections.

B) *Geographical Variation*
The significant geographical variation in genome size was revealed for several amphibian species (Licht and Lowcock, 1991; Murphy et al., 1997; Litvinchuk et al., 1999, 2001b). In a few cases, differences (RD) exceeded 8%. However, in the majority of species studied, such differences were about 1% (Licht and Lowckock, 1991; Borkin et al., 1997, 2000, 2001, 2003; Litvinchuk et al., 1997, 1999, 2001b, 2003; our data). In *Salamandrella keyserlingii*, the maximum genome size difference (RD = 4.5%) was found between samples from the Khandyga (Yakutia Republic) and Kedrovaya Pad' Reserve (Primorsky Territory). The average differences (RD) between the "Euro-Siberian" and the "Primorsky" sample groups of the species were equal to 3.2%.

3) Interspecies differences: developmental and karyological correlations

Eleven species of the family Hynobiidae may be divided into two groups by their genome size. Two species of the genus *Onychodactylus* form a group with the largest genomes (104-108 pg). They also have the longest embryonic and larval development periods (Table 3), as well as the greatest number of chromosomes (Table 4).

Another group includes the remaining nine species (33-67 pg). Among them, *Salamandrella keyserlingii* has the largest genome size, and the seven species from the genera *Hynobius* and *Batrachuperus* have smaller sizes. *Ranodon sibiricus* has an intermediate genome size. Such a distribution of genome sizes in the second group does not seem to be associated with ovum diameter, and, perhaps, with time of embryonic and larval development (Table 3).

The comparison of genome size values in the second group with karyological data evidenced no signifi-

cant relations between the nuclear DNA content and diploid chromosome numbers (Table 4). Nevertheless, we found the positive correlation (r = 0.9998) between genome size and uniarmed macrochromosome numbers.

4) Intergeneric relationships

Based on recent studies (Fei and Ye, 2000a; Fu et al., 2001), approximately eight or ten genera of the hynobiids could be recognized. The most speciose genus, *Hynobius,* consists of about 24 species, which may be arranged into three subgenera (Matsui et al., 1992; Mizuno et al., 1995; Borkin, 1999), namely *Pseudosalamandra* (7 species from Japan and Taiwan), *Satobius* (1 species from Hokkaido Island), and *Hynobius* (11 species from Japan, and, perhaps, 5 species from Korea and China). The family also includes the genera *Liua* (1 species), *Onychodactylus* (2 species), *Pachyhynobius* (1 species), *Protohynobius* (1 species), *Pseudohynobius* (2 species), *Ranodon* (1 species), *Salamandrella* (1 species, which penetrates to eastern Europe), and *Batrachuperus* (sensu lato) (about 9 species). The taxonomic position of *Ranodon*, *Liua*, and *Pseudohynobius* was discussed (Fei and Ye, 2000b; Kuzmin and Thiesmeier, 2001). Based on mitochondrial DNA study, T. Papenfuss (Pers. comm. in Fu et al., 2001) showed that the genus *Batrachuperus* is paraphyletic, and consists of two groups with distinct geographic distributions. The Eastern (Chinese) group belongs to *Batrachuperus* (sensu stricto) and consists of about six species (Fei and Ye, 2000b; Fu et al., 2001; Song et al., 2001). The western (Iran and Afganistan) group includes two or three species (Stöck, 1999), and may be allocated to *Paradactylodon*.

Various authors suggested several configurations of evolutionary relationships among hynobiids. For instance, based on reproductive biology characters, Thorn (1969) proposed to recognize two families: Ranodontidae, with the genus *Ranodon* only, and Hynobiidae, with remaining genera. Using a set of morphological and biological data, Zhao and Hu (1984) separated two "natural" groups among Chinese species: the *Hynobius* group with predominantly terrestrial species (*Hynobius* and *Salamandrella*), and the *Ranodon* group with predominantly aquatic inhabitants (*Ranodon*, *Onychodactylus*, *Batrachuperus*, and *Liua*). Later, Zhao and Zhang (1985) assigned the genus *Pachyhynobius* to a third group. Combining morphological characters and mitochondrial DNA data, Larson and Dimmick (1993) found the closest relationships between the genera *Salamandrella* and *Hynobius*, thus confirming the traditional acceptance of the similarity of these taxa. However, the genus *Onychodactylus* was more closely related to that lineage, whereas *Batrachuperus* (the eastern group) proved to be more distant. Recently, Fei and Ye (2000a) have erected a new subfamily for the newly discovered *Protohynobius puxiongensis*, whereas all other hynobiids were allocated to another subfamily.

Genome size data are not in agreement with all these suggestions, which did not recognize separate position of the genus *Onychodactylus*. Apart from the largest genome size, distincton of the genus was also supported by morphological and karyological data (Morescalchi et al., 1979; Olmo, 1983; Kohno et al., 1991; Iizuka, Yazawa, 1994; Kuro-o et al., 2000; Litvinchuk and Borkin, 2003).

5) Taxonomic considerations

Based on the intraspecific analysis, Bassarukin and Borkin (1984), and Borkin (1994) outlined the peculiarities of *Salamandrella keyserlingii* from the southern part of the Russian Far East. Moreover, these authors suggested that local populations would be considered as a geographic race of the species (the species type territory is the Kultuk Village, Baikal Lake, Irkutsk Province, Russia; restricted by Borkin, 1994). Indeed, the "Euro-Siberian" and "Primorsky" groups of populations are different in allozymes (Litvinchuk et al., 2001a), in some morphological characters (Ostashko, 1981; Bassarukin and Borkin, 1984; Borkin, 1994; Litvinchuk and Borkin, 2003), in breeding sites (Kuzmin, 1990), and in the shape of egg sacs and time of larval development (Korotkov, 1977; Bassarukin and Borkin, 1984; Sapozhnikov, 1990; Vorobyeva et al., 1999). Therefore, geographic differences in genome size revealed by us are in concert with differences in other characters. Based on a concordance of various characters, including genome size, we would recognize a distinct status of the "Primorsky" samples, at least, of a subspecific rank. Formerly, Nikolsky (1906) and Dybowski (1928) have coined the names *Salamandrella keyserlingii* var. tridactyla and *Salamandrella keyserlingii* var. kalinowskiana, respectively, for animals from the Russian Far East. Obviously, the first name has the priority. Therefore, populations from Russian Far East (Primorsky Territory) should be named *Salamandrella keyserlingii tridactyla* Nikolsky, 1906.

The range of *Ranodon sibiricus* is quite limited. Nevertheless, it consists of several semi-isolated areas (Brushko et al., 1988; Kuzmin et al., 1998; our data). The populations from the upper parts of Borokhudzir and Oy-Saz Rivers are separated from each other by a mountain range. Therefore, it is not surprising that the genome size difference (RD) between them is relatively large (2.2%). However, geographical variation in the species is poorly studied, and so the taxonomic value of that difference is still unclear.

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Anomalous (?) Nocturnal Feeding by the Agamid Lizard *Calotes emma* in Northeastern Thailand

WILLIAM H. SCHAEDLA

Department of Biology, Arizona State University, P.O. Box 871501 Tempe, Arizona 85287-1501, U.S.A.
E-mail: schaedla@asu.edu

Abstract. - I observed feeding by the Agamid lizard *Calotes emma* during the early part of the Thai monsoon season. During this period, one individual took advantage of swarming termite reproductives and fed nocturnally. Nocturnal activity has not been reported for this genus. The lizard's behavior may have resulted from conditions created by artificial lighting. Alternately, it may constitute a normal response to a rich annually-available food resource.

Key words. - *Calotes emma,* feeding, termites, nocturnal, atypical behavior.

Introduction

Agamid lizards belonging to the genus *Calotes* are widely distributed throughout South and Southeast Asia. They are characterized by semi-arboreal or arboreal behavior, strongly diurnal activity patterns, and insectivorous diets (Erdelen, 1988; Günther, 1864; Subba Rao 1970, 1975; and Subba Rao and Rajabai, 1972).

Calotes emma is a typical member of the genus. The species occurs from Assam through Yunnan in the north, and Peninsular Thailand in the south. It prefers moist forested habitat and is arboreal to semi-arboreal it its habits (Günther, 1864). Here I report observations of *C. emma* feeding at night in a manner apparently contrary to norms for the genus.

Methods

This study took place at the Sakaerat Environmental Research Station. Sakaerat is a scientific and educational facility located in Northeastern Thailand at 14° 30.46' N Latitude by 101° 55.92' E Longitude. The station grounds cover approximately 80 km^2.

Small and medium-sized wildlife is plentiful in the area. As of this writing, 70 species of mammals, 50 species of birds, and 25 species of amphibians have been recorded from Sakaerat. Reptile fauna is also abundant ~82 species are known to occur (Lawanyawatna and Schaedla, 2000). Of the reptiles, *C. emma* is among the most common because of the station's abundant forest cover.

Seasonal (monsoonal) and perennial dipterocarp forests comprise the bulk of Sakaerat's habitats. I worked specifically in an area of Dry Evergreen Forest, which is a Dipterocarp mosaic containing other floral components. It is a four storied forest. The upper story extends from 21 to 40 m in height and consists mostly of *Hopea ferrea*, *H. odorata*, *Shorea sericeiflora*, and *Irvingia malayana*. The middle story ranges from 15 to 20 m in height and contains *Hydrocarpus ilicifolius*, *Memocylon ovatum*, and *Walsura trichostemnon*. The lower story is between 4 and 24 m in height and is characterized by *Baccaurea sapida*, *Apodytes dimidiate*, and *Olea salicifolia*. Undergrowth is less than 4 m from the ground, leafy, and composed mainly of *Ardisia*, *Canthium*, and *Clausena*.

Average humidity at Sakaerat runs about 76% over the course of the year. Average annual precipitation is 1,222 millimeters, and average annual temperature is 26°C. March is the hottest month with a maximum recorded high of 37°C. January is the coolest with a minimum recorded low of 8°C. Sakaerat generally experiences a 3.5 month long rainy season that lasts from early June through mid September. Conversely, rainfall is rare from December through February (Tongyai, 1980).

I made behavioral observations of Sakaerat's *Calotes emma* on the evenings of 7, 10, and 12 June, 2001. These dates followed the onset of the local monsoon season, but were not monsoon days themselves. Weather conditions were overcast, but there was no heavy or sustained precipitation. Rainfall was light and intermittent, accompanied by occasional lightning. Ambient temperature was moderate, ranging from 27° to 30°C.

My observations took place from approximately 6:00 PM (dusk) to 9:00 PM. I watched from an area in a semi-secluded part of the research station. My vantage was the front porch of a bungalow near Sakaerat's station headquarters, but offset in the forest and away from the main complex of office, visitor's center, cafeteria, and general housing. This area is dimly lit by two overhead fluorescent lights attached to the sides of buildings. These lights attract large numbers of insects, especially during seasonal monsoon periods. In particular, termite alates (winged reproductives) were present in high num-

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bers on the evenings I observed. Large swarms of *Odontotermes* sp. and *Macrotermes* sp. clouded the local area and eventually dropped to the ground.

When termites fell to the ground, I observed a single *C. emma* feeding them. The lizard was present all three rainless nights, and seemed unperturbed by my presence. It was there from dusk, or before, to nearly 9:00 PM on all three evenings. It was active, and its behavior was restricted to the terrestrial environment. It did not climb nearby trees or the sides of wooden buildings. All of its movements were directed; it displayed no signs of disorientation in the relative darkness of its surroundings. On the contrary, it focused on the termite alates and fed vigorously on them as they landed.

On June 10, I captured the lizard to verify its identity as *C. emma*. It had been correctly identified and was a mature female. Her stomach was distended from termite consumption, but she was not visibly gravid with eggs.

In addition to the lizard, other predators feeding on the termite alates included toads (*Bufo melanostictus*), geckoes (*Cyrtodactylus spp.*), and centipedes (*Scolopendramorpha*).

Discussion

Little is known about the exact feeding preferences of *C. emma*. However, some indication of its diet might be inferred from studies of a closely related arboreal species. Subba Rao (1972) found that *C. nemoricola* in India fed mostly on ants, while *Sitana ponticeriana*, an unrelated ground-dwelling lizard, fed on termites. In another study he found that *C. nemoricola* consumed a wide variety of invertebrates ranging from beetles, to gastropods, to earthworms. Analysis of gut contents showed a predominance of ants but no termites. He also noted a distinct absence of flying insects in the lizards' stomachs (Subba Rao, 1975). Hence, feeding on winged termites by *C. emma* may represent a departure from its normal dietary habits.

Likewise, nocturnal feeding has not been reported in the literature surrounding *Calotes*. In fact, members of the genus are usually active only during the day (Erdelen, 1988; Günther, 1864; Subba Rao 1970, 1975; and Subba Rao and Rajabai, 1972). *C. emma* at Sakaerat is decidedly diurnal in its habits. At night they tend to sleep on the ends of low-hanging tree branches. Spotlighting does not wake them and they can be captured easily by anyone walking through the forest with a headlamp. I have worked at Sakaerat for three years, and, with the exception of the observations reported herein, I have never seen them active at night.

Calotes is apparently physiologically predisposed towards diurnal activity. Light has a positive affect on both the pituitary and the hypothalmamo-neuro secretory systems of *C. versicolor* (Banerjee, 1972). However, Kar (1987) found that day length (photoperiod) played a less important role than ambient temperature in scale regeneration by *C. versicolor*. He speculated this happens because the lizards' thyroid activity is elevated by heat, rather than light.

Evening temperatures were warm on the nights I made my observations. The lizard I observed may have been able to extend her activity because of this. It is also possible that the lack of sunlight was mitigated by the presence of overhead florescent lights (albeit dim). My subject may simply have been disrupted from its normal circadian routine by the local environment. Some support for this possibility comes for another observational study. Subba Rao et al. (1984) noted that abrupt changes in light intensity, temperature, and relative humidity during a total solar eclipse actually stimulated activity in *C. versicolor*.

Of course, the feeding I observed may have been part of *C. emma*'s normal behavioral regime. Termite alates constitute a rich, but seasonally discrete food source, induced by the onset of the monsoons. They are available in great numbers at specific times of the year, and they attract a wide variety of predators, including retiles. It is therefore possible that *C. emma* takes advantage of the bonanza via seasonal changes in behavior. Whatever the case, nocturnal feeding by *C. emma* is unusual and unreported. Even if not anomalous it deserves future attention.

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Karyological Studies on Amphibians in China

YUHUA YANG

Molecular Biology Labortary, Department of Bioengineering, Sichuan University, Chengdu, 610064, R.P.China

Abstract. - Since 1978, 79 species of anurans have been studied karyotypically using conventional Giemsa staining and various banding techniques. The chromosome numbers are 2n=22-64 and the karyotypes are variable. The homomorphic and heteromorphic sex chromosomes of some species have been identified.The mitotic and meiotic chromosomes of 14 species in two families of Urodela have also been investigated. The family Hynobiidae is karyotypically more primitive than the family Salamandridae.

Key words. - Karyology, amphibian, Anura, Urodela.

Introduction

Karyological studies of amphibians in China were pioneeered by two scholars. In 1952, famous cytologist T. C. Hsu, an American of Chinese origin, developed the hypotonic technique for chromosome separation and observation. In 1956, cytogeneticist J. H. Tjio, a Swede of Chinese origin, reported that the number of human chromosomes is 46, not 48. In China, karyological studies of amphibians began in 1978. Ninety-three species of amphibians have been studied so far, about 42% of the 220 living amphibian species in China (Table 1).

Changes of chromosome numbers. - Kuramoto (1990) summarized the chromosome numbers of 983 species of anurans from 21 families (2n=14-64). Chromosome number changes occurred in 12 of 21 families with polyploids in some species. In China, the chromosome numbers of 79 species from seven families are 22-64 and variations of chromosome numbers were found in four genera, three families (Table 2).

Only two species in the family Discoglossidae have been studied: *Bombina orientalis* and *B. maxima*. Tian and Hu (1985) subdivided the genus *Bombina* into two subgenera, *Bombina* and *Glandula*. *Bombina* (*B.*) *orientalis* has 2n=28 chromosomes (Zhao, 1986), consistent with the chromosome number of *Discoglossus pictus* in Europe (Morescalchi, 1965; Schmid et al., 1987). *Bombina* (*G.*) *maxima* has 2n=24 chromosomes (Jiang et al., 1984), as reported by Okumoto (1974) and Schmid et al. (1987).

The geography of the Hengduan Mountain Ranges greatly influence the evolution of pelobatid frogs, providing refugia for some species as well as discontinuous population distributions that promote allopatric speciation (Yang et al., 1983; Hu et al., 1985). The pelobatids distributed in the Hengduan Mountain region have distinct morphological differences adaptive to the unusual geographic conditions. These species belong to two subfamilies, Megophryinae (*Brachytarsophrys* and *Atympanophrys*) and Oreolalaxinae (*Scutiger*, *Vibrissaphora*, *Leptobrachium*, and *Oreolalax*). Available karyotypical information showed that species studied have 2n=26 chromosomes, but karyotypical differentiations are prominent in the family. The subgenus *Vibrissaphora* is the most specialized, all five species have 2n=26, consisting of six pairs of large chromosomes and seven pairs of small ones, NF=52 and one stable secondary constriction is located in 6q (in the NoRs region; Zhao et al., 1983). The karyotypes of three species in genus *Scutiger* are similar to those of subgenus *Vibrissaphora*, except the secondary constriction located in 2P not in 6q. Polymorphic chromosome number occured in Oreolalax. Two of the three specimens of *O. schmidti* are 2n=28 and one is 2n=26 (Zheng andWu, 1989). A similar phenomenon was found in *O. liangbeiensis* and C-banding showed that the extra pair of small chromosomes is C-band negative and not B chromosome (Li et al., 1990). Polymorphic chromosome numbers were also found in three genera of Megophryinae. Wu (1987) observed one male triploid in *Atympanophrys shapingensis*. Tan et al. (1987) reported the karyotypes of *Brachytarsophrys carinensis*. Among 12 individuals examined, seven males and one female have 2n=26, three males have 2n=27, and the remaining male has 2n=28. The extra chromosomes are metacentric and between No.10 and No.11 in size. In addition, there are four pairs of small chromosomes which are telocentric in the2n=26 karyotype and two pairs of small telocentric chromosomes were observed in *M. omeimontis* (Wu, 1987; Zheng and Wu, 1989).

The karotypes of pelobatids reported by foreign authors are 2n=26, NF=52 with no polymorphic chromosome numbers found, except *Leptolalax pelodytoides* with 2n=24 (Morescalchi, 1973; Morescalchi et al. 1977; Schmid, 1980, 1987). It is interesting that a special karyotype was observed in *Rana phrynoides* distributed in Hengduan Mountains. In this species, 2n=64 consisting of all telocentric chromosomes. Only one homologous pair of NORs being found in interstitial

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Table 1. A list of amphibian species studied karyologically.

Famlies	Number of species Known	Number of species studied	Number of species Banded
Anura:			
Discoglossidae	4	2	0
Pleobatidae	46	18	12
Bufonidae	13	4	4
Hylidae	6	4	1
Ranidae	77	35	24
Rhacophoridae	32	7	3
Microhylidae	14	9	4
Total anurans	192	79	48
Caudata:			
Hynobiidae	17	7	0
Salamandridae	17	7	2
Total caudates	34	14	2

segment of No.20 chromosome, i.e, position of the sole secondary constriction, and No.32 being sat-chromosomes (Liu and Zan, 1984; Wu and Zhao, 1984). This karyotype is unique for anurans.

Karyological Studies on wood frogs in China. - In China, wood frogs include five species (*R. altaica*, *R. amurensis*, *R. japonica*, *R. chaochiaoensis*, and *R. chensinensis*; Tian and Jiang, 1986). *Rana chensinensis* had been called *R. temproaria chensinensis* (Pope and Boring, 1940; Liu and Hu, 1961). Wu (1981) reported the karyotype of *R. chensinensis* from Beijing, which has 2n=24 chromosomes, including six pairs of large chromosomes (relative length>7%) and six pairs of small ones (relative length<6%), while *R. temporaria* in Europe has 2n=26 (Guillemin, 1967), including five pairs of large chromosomes and eight pairs of small ones. Consequently, he suggested that R. chensinensis should be a good species, not a subspecies of *R. temporaria*. Wei et al. (1990) compared the C-bands and NORs between *R. chensinensis* from type locality and *R. temporaria* in Europe. As a result, in the former species, centric C-bands located in Nos. 9 and 10 chromosomes and telocentric C-bands in the terminations of a few chromosomes, 28 interstitial C-bands, one pair of standard NORs in 11q, and small additional NORs are found. However, in the latter species, both centric and telocentric C-bands are located in all chromosomes and only three interstitial C-bands and 1 pair of NORs in 10q were developed (Schmid, 1978). Evidently, this comparison supports Wu's suggestion.

Jiang et al. (1984), Luo and Li (1985) and Ma (1987) indicated that *R. chensinensis* from different localities have the same 2n=24 pattern, but the numbers of subtelocentric chromosomes and the positions of secondary constrictionas are locality specific by comparing the karyotypes of *R. chensinensis* from Beijing, Qingdao, Lanzhou, Harbin, Hongyuan and Yanbei. Consequently, it was suggested that *R. chensinensis* might contain different subspecies .

The five species of wood frogs have 2n=24 or 2n=26 chromosomes and may be divided into two groups: *R. japonica*, *R. chaochiaoensis* and *R. amurensis* belong to 2n=26 group and *R. chensinensis* and *R. altaica* to 2n=24 group. The karyotypic differences between two groups are listed in Table 3.

Rana japonica from Hiroshima, Japan has 2n=26 chromosomes, Nos. 8 and 9 are subtelocentric and the secondary constriction is located in 9q; *R. amurensis coreana* from Korea has 2n=26, Nos. 10 and 13 subtelocentric and secondary constriction in 9q; while *R. chensinensis* from Hokkaido, Japan has 2n=24, No.11 is subtelocentric and the secondary constriction in 10q (Nishioka, et al., 1987). Matsui (1991) described *R. chensinensis* from Hokkaido as a new species, *R. pirica*, based on morphometric and electrophoretic studies.

The No.6 chromosome of the species having 2n=24 is nearly the same in relative length as the sum of chromosomes No.11 and No.12 or No.13 of the species with 26 chromosomes, For instance, the average relative length of No.6 chromosomes of *R. chensinensis* and *R. altaica* is 8.19, while the average relative lengths of Nos.11, 12 and 13 chromosomes of the other three species are 4.52,4.31 and 3.82 respectively. In addition, it is clear from Table 3 that there are more subtelocentric chromosomes and secondary constrictions in the species having 26 chromosomes than those in the species having 24 chromosomes, and they are concerned with small chromosomes. Accordingly, it is speculated that all wood frog species would have a common ancestor, from which the species having 26 chromosomes were derived and the species having 24 chromosomes evolved via fusion of two pairs of small chromosomes of the former. Then, the species possessing

Table 2. A summary of chromosome numbers of 79 anuran species.
* = Polymorphic chromosome number occurs in some species.

Taxon	Number of species					
	22	24	26	28	64	Total
Discoglossidae						
Bombina	-	1	-	1	-	2
Pelobatidae						
Atympanophrys	-	-	1	-	-	1
Brachytarsophy	-	-	1	-	-	1
*Megophrys**	-	-	2	-	-	2
*Oreolalax**	-	-	6	-	-	6
Scutiger	-	-	3	-	-	3
Vibrissaphora	-	-	5	-	-	5
Bufonidae						
Bufo	4	-	-	-	-	4
Hylidae						
Hyla	-	4	2	-	-	6
Ranidae						
Rana	1	2	21	-	1	26
Amolops	-	-	7	-	-	7
Ooeidozyga	-	-	2	-	-	2
Altirana	-	-	1	-	-	1
Rhacophoridae						
Rhacophorus	-	-	5	-	-	5
Philautus	-	-	1	-	-	1
Polypedates	-	-	1	-	-	1
Microhylidae						
Microhyla	-	4	1	-	-	5
Kaloula	-	-	-	1	-	1
Kalophrynus	-	-	1	-	-	1
Total	5	11	60	2	1	79

different subtelocentric chromosomes and secondary constriction positions were developed into two groups through inversions and translocations. The high resolution R-bands of *R. japonica* were prepared and analyzed (Heng, 1984), providing a practical technique for studying karyotypic evolution of amphibians.

Sex chromosomes and sex-determining mechanisms.- The first successful demonstration of sex-determining mechanism was made by making use of reversal and breeding experiments (Humphrey, 1942, 1945, 1957). The applications of cytogenetic techniques, such as C-banding, quinacrine mustard staining, Ag-NORs staining and in situ hybridization of nucleic acids, have been helpful to the investigations on sex chromosomes and sex-determining mechanisms in amphibians. So far, eleven species with cytologically detected sex chromosomes, including XY and ZW systems, even an OW/OO system of sex determination and multiple sex chromosomes in one genome(Schmid et al., 1992) were discovered. Few sex-specific chromosome pairs in heterogametic individuals are heteromorphic and most of them are homomorphic.

The homomorphic chromosome pair No.4 in *Rana esculenta* was identified as sex-specific chromosomes of XX/XY type by BrdU replication banding technique. All males have an extremely late-replication band in the long arm of Y, which is lacking in the X (Schempp and Schmid, 1981). The homomorphic chromosome pair No.10 in *Bufo gargarizans* was demonstrated to be sex chromosomes of ZZ/ZW type. The Z chromosomes in all males replicated synchronously, while Z and W chromosomes of females revealed heteromorphic replication bands at the late replication stage. There was a replication band on W chromosome's long arm and Z chromosome lacked the band (Wen et al., 1982;Shang and Deng, 1982). Similarly, the chromosome No.6 pair in *Bufo raddei* was identified as XX/XY sex chromosomes (Deng and Shang, 1984) and the No.9 chromosomes of *Rana nigromaculata* as XX/XY sex chromosomes (Wu and Zhang, 1985). The sex chromosomes of species mentioned above are homomorphic and could only be recognized by BrdU replication banding. So they are at the initial stage of sex chromosome differentiation.

The Y or Z chromosomes of homomorphic sex chromosomes in some anurans heterochromatinized so

Table 3. karyotypic comparison between wood frog groups.

Species	2N	Subtelocentric pair(s)	Position of S.C.
R. japonica	26	No.7 or No.9	2-5p,6-7q
R. chaochiaoensis	26	No.8 Nos.9,10,12,13	5-7p,8q,10p
R. amurensis	26		8q
R. chensinensis (from type locality)	24	No.9	11q
R. altaica	24	--	1q

highly that they could be recognized by C-banding or other specific staining of constitutive heterochromatin, for example, the XX/XY sex chromosomes in genus *Triturus* (Schmid, et al., 1979). Chinese scholars Wu and Chen (unpublished data) determined the homomorphic chromosome pair No.9 as XX/XY sex chromosomes in *Rana margaratae* using C-banding and quinacrine mustard staining. There is one interstitial C-band, i.e, the brightest fluorescense band, on both No.9 chromosomes in females. The interstitial C-band is located only in one No.9 chromosome, while one telocentric C-band in the other No.9 chromosome shows no fluorescense differentiation.

The first-discovered highly heteromorphic ZW type sex chromosomes occured in *Pyxicephalus adspersus* (Schmid, 1980). The W chromosome is much smaller than Z chromosome and its short arm is completely heterochromatic. Wu and Zhao (1984) and Wu et al. (1987) demonstrated that *Amolops mantzorum* has well-differentiated XY type sex chromosomes,the Y chromosome is subtelocentric and mainly composed of euchromatin, but has strong C-band in the middle of long arm and X chromosome is metacentric by conventional Giemsa staining and C-banding methods.

Karyological studied in urodeles. - Only two species were studied by C-banding and the others by conventional Giemsa staining. The karyotypic comparisons are listed in Table 4. The family Hynobiidae has a wide geographical distribution. Twenty-six species in five genera out of more than 34 species in eight genera have been studied karyologically. The chromosome number vary from 40 to 80 . Twelve species in *Hynobius* and one in *Salamandrella* had been studied by C-banding, Ag-NORs staining, and R-banding. The relationships in the two genera were discussed by comparing banded karyotypes and Southern hybridizations. It is suggested that the family is the most primitive living caudate (Morescalchi, 1973; Kohno et al., 1991).The same conclusion is derived from morphological comparisons (Zhao and Hu, 1984).

There are 17 species in seven genera in Hynobiidae known from China. The family can be divided into two groups: *Hynobius* group and *Ranodon* group. The *Ranodon* group evolved by adaptation towards two different life-forms: aquatic and terrestrial. Liua and *Batrachuperus* are aquatic and are closely related. Table 4 shows that seven species have high chromosome numbers: 2n=62-68. Their karyotypes are bimodal and symmetrical, with more microchromosomes (Yang, 1992). *Salamandrella keyserlingii* has 2n=62 chromosomes, the karyotype formula being 4M + 2SM + 10ST + 10T + 36 m (Wang et al., 1983) in accordance with that reported by Morescalchi (1975), Morescalchi et al. (1979), Grafodatsky et al. (1978), Kuro-o(1986), and Ikebe et al. (1990). The bivalent number in cells of male *Batrachuperus pinchonii* in diakinesis is 31. We expect the diploid chromosome number to be 2n=62 (Yang and Zhao, 1984), but this species also has 2n=66 chromosomes (Kuro-o et al., unpublished data). There is little detailed information on the cause of the difference.

The karyotypic differentiation of Hynobiidae is more complex. First, variations in diploid chromosome number occurred not only at the intergeneric level,but also at the intrageneric level. For instance, *Salamandrella* has 2n=62, *Batrachuperus* 2n=62-68, both *Liua* and *Pachyhynobius* 2n=64. Secondly, the numbers of microchromosomes vary from 36 to 46. Finally, the morphology of microchromosomes are variable. The numbers of M, SM, and ST are species-specific. Telocentric macrochromosomes were found in *S. keyserlingii, L. shihi* and *P. shangchengensis*, but not in *Batrachuperus*. The *L. shihi* and *P. shangchengensis* studied were from the type localities (Zhao and Hu, 1983; Fei et al., 1983). Both two species have 2n=64 chromosomes, different from the known genera. However, they are different in morphology of macrochromosome and microchromosome number (Table 4) . Therefore, the cytogenetic data provide evidence supporting those genera and species.

There are four species in *Batrachuperus*. *Batrachuperus karlschmidti* and *B. yenyuanensis* are only found higher than 3000M in the Hengduan Mountains, having 2n=68, no telocentric macromosomes and 44 and 46 microchromosomes respectively. *Batrachuperus pinchonii* and *B. tibetanus* distributed higher than 1600M of Hengduan Mountains and adjacent areas have 2n=62. Obviously, the karyotypic differ-

Table 4. Karyological comparisons of urodela in China. **M**-metacentric macrochromosomes; **SM**-submetacentric macrochromosomes; **ST**-subtelocentric macrochromosomes; **T**-telocentric macrochromosomes; **m**-microchromosomes.

Species	2N	Number of Bivalent	M	SM	ST	T	m	Band
Hynobiidae								
Salamandrella keyserlingii	62		4	2	10	10	36	--
Batrachuperus karlschmidti	68		6	-	18	-	44	--
B. yenyuanensis	68		4	2	16	-	46	--
B. pinchonii	(62)	31						--
B. tibetanus	62							--
Liua shihi	64		6	2	4	10	42	--
Pachyhynobius shangchengensis	64		4	-	2	18	40	--
Salamandridae								
Tylototriton kweichowensis	24	12	16	6	2	-	-	--
T. verrucosus	(24)	12						--
Cynops cyanurus yunnanensis	(24)	12						--
C. orientalis	24	12	16	8	-	-	-	C
Paramesotriton chinensis	(24)	12						--
Pachytriton brevips	24		16	8	-	-	-	C
P. labiatum	(24)							--

entiations in *Batrachuperus* are in conformity with the geographic distribution.

Salamandridae is the advanced family in Caudata either from the viewpoint of karyotypic information or from that of morphological characteristics (Morescalchi, 1973, 1975, 1979; Zhao and Hu, 1984; Yang, 1992).There are five genera of Salamandridae found in China: *Tylototriton*, *Echinotriton*, *Cynops*, *Paramesotriton*, and *Pachytriton*. Of the five genera, *Tylototriton* is the most primitive and *Pachytriton* the most advanced . The seven species studied in five genera have the same chromosome number, 2n=24, without microchromosomes. The karyotypes are unimodal and symmetrical (Table 3). Interspecific differences were found in *Tylototriton*. The karyotypic formula of *T. kweichawensis* is 16M+6SM+2ST, the same as that of *T. verrucosus*. However, Nos. 6, 8 and 11 are submetacentric and no secondary constriction was found in the former (Yang, 1990), while Nos.6, 7 and 11 are submetacentric and secondary constriction were found at every chromosomes except No.12 in the latter (Seto et al., 1982). *Echinotriton andersoni* has 2n=24 chromosomes, 14M + 8SM+ 2ST, one more submetacentric chromosome pair than both *T. kweichowcensis* and *T.verrucosus* (Seto et al., 1982). In addition, the relative length of chromosome No. 1 is the longest and that of No.12 the shortest in *E. andersoni* among the three species mentioned above. The karyotypic formulas of *Pachytriton brevipes* and *Cynops orientalis* are nearly identical and only the differences of C-band patterns are found (Zhu and Wei, 1981).

The predominant mode of karyotypic evolution in Caudata is that the unimodal symmetrical karyotypes with fewer chromosome number are derived from the bimodal and asymmetrical karyotypes with more chromosome number, via Robertsonian centric fusions and pericentric inversions (Morescalchi, 1975). Robertsonian centric fusions, which could occur between telocentric macrochromosomes, between stable microchromosomes, and between telocentric macrochromosomes and stable microchromosomes, cause reduction of the diploid number and the microchromosome number and increase of the metacentric chromosomes. Consequently, the karyotypes tend toward stability. Pericentric inversions do not change the diploid number, but could increase the number of metacentric chromosomes and the stability of karyotypes.

There are some differences in the evolutionary trends of Hynobiidae and Salamandridae. The karyotypic evolution in Hynobiidae involves Robertsonian centric fusion as well as pericentric inversion. However, the phylogeny of the family could not be established on the available data. It is obvious that the karyotypes of Salamandridae are more stable than those of Hynobiidae. Morescalchi (1975) proposed that all species studied possess similar karyotypes that differ very little even at the intergeneric level. The differences between the karyotypes mainly lie in the absolute size of chromosomes and quantity of DNA. Accordingly, the karyotypic diversity among the species has chiefly resulted from pericentric inversions and reciprocal translocations that result in differences between individual chromosomes by changing the telocentric chromosomes into metacentric ones or changing the metacentric chromosomes into submetacentric, subtelocentric and telocentric chromosomes.

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The History of the Journal *Asiatic Herpetological Research*

THEODORE J. PAPENFUSS

Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720, USA

The origins of Asiatic Herpetological Research go back 34 years. Our present editor, Professor Ermi Zhao started a scientific periodical, *Materials for Herpetological Research,* in 1972. Four issues were published, the last in 1978 (Zhao and Adler, 1993). The text of all articles was in Chinese only. The four issues were produced by the Sichuan Biological Research Institute (now the Chengdu Institute of Biology). *Materials* was followed by *Acta Herpetologica Sinica,* which was also edited by Zhao. There were two series between 1979 and 1987. The "old series" consisted of six volumes published from 1979-1982 and the "new series" from 1982-1987 (Zhao and Adler, 1993). The articles were in Chinese, but English titles and often, English abstracts were included.

Volume 1 of a new journal, *Chinese Herpetological Research,* also edited by Zhao, was published in Chongqing for the Chinese Society for the Study of Amphibians and Reptiles, with Zhao continuing as editor. In 1988 Zhao visited the Museum of Vertebrate Zoology, University of California at Berkeley as part of his collaboration with J. Robert Macey and I. The MVZ's single Mac Classic computer that could be used for desktop publishing impressed him. At Zhao's request we agreed to transfer printing and distribution from China to Berkeley. Macey and I also agreed to serve as Associate Editors and to help assemble an international editorial board. We changed the name of the journal to *Asiatic Herpetological Research* with volume 3 in 1990. With this volume 10, our journal will return to the Chengdu Institute of Biology for printing and distribution. The quality of journals published in China is now of world standard and the Internet, unknown in 1988, allows for easy electronic transfer of manuscripts, and easy editing

Although our society is not large in membership, it is very international. We have published articles by authors from 29 countries. Fourteen new species of amphibians and reptiles have been described since 1987. We organized the First Asian Herpetology Meeting, held in China in 1992, the Second Asian Herpetology Meeting held in Turkmenistan in 1995, the Third Asian Herpetology Meeting held in Kazakhstan in 1998, and a Fourth Asian Herpetology Meeting in 1991 again in China.

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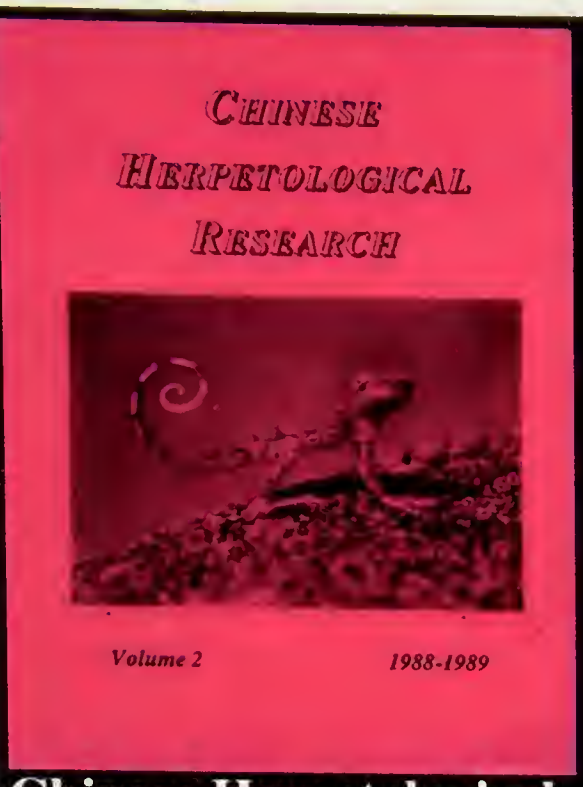

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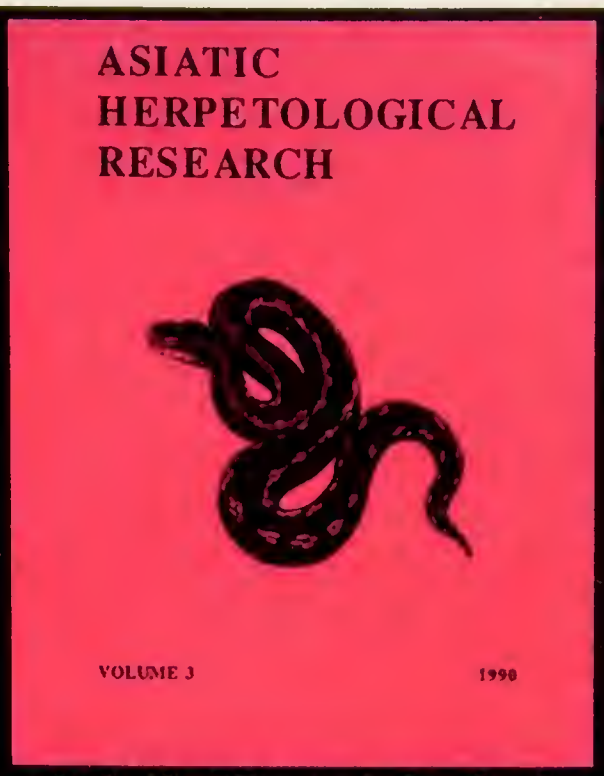

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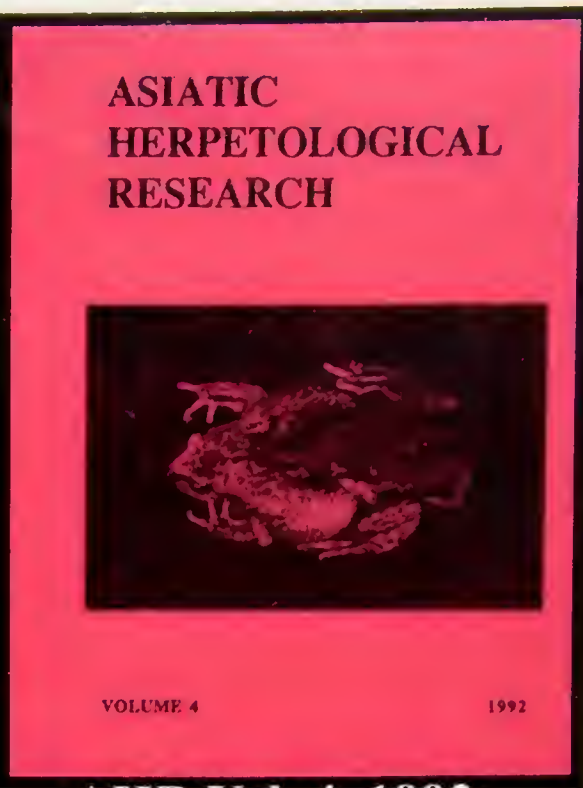

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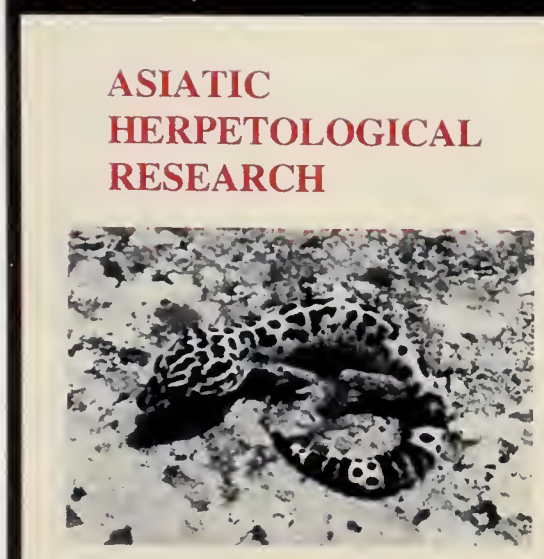

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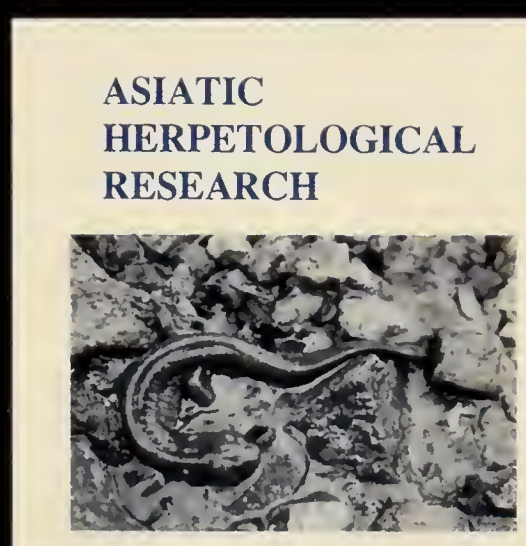

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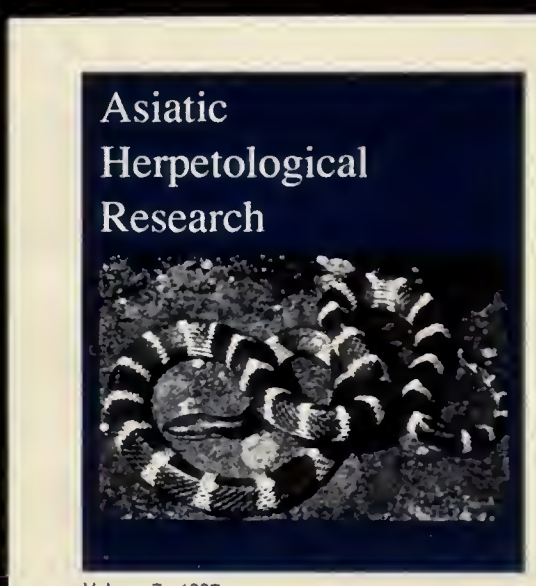

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Guidelines for Manuscript Preparation and Submission

Summary

Manuscripts must:

1) be written in English.

2) be of letter quality (laser printed or typewritten on bond paper).

3) include camera ready figures (if any).

4) include complete and accurate literature citations.

5) include complete and accurate localities with latitude and longitude.

6) include a camera ready map illustrating regions discussed (when applicable).

Tips for electronic submission

• Do not use multiple **tabs** or **spaces** to separate columns in tables.

Either use the table feature of your word processor, a spreadsheet program (e.g. Excel), or separate columns with a **single tab**.

Table 1.Example of improper use of multiple tabs to separate columns in a table.

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• Do not type authors names in all capitals in literature cited.

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Please use only simple formatting limited to *italics*, **boldface,** and underline.

Manuscripts failing to meet these criteria will be returned without review for correction.

Purpose and Content

Asiatic Herpetological Research publishes articles concerning but not limited to Asian herpetology. The editors encourage publications from all countries in an attempt to create an open forum for the discussion of Asian herpetological research.

Articles should be in standard scientific format and style. The following sections should be included:

Title

The title should reflect the general content of the article in as few words as possible. The editors encourage titles that summarize the main findings of the article.

Names and Addresses

The names and addresses of all authors must be complete enough to allow postal correspondence. Please include email and World Wide Web addresses if applicable.

Abstract

The abstract should briefly summarize the nature of the research, its results, and the main conclusions. Abstracts should be less than 300 words.

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Key words provide an index for the filing of articles. Key words provide the following information (when applicable): 1) Taxonomy (e.g. Reptilia, Squamata, Gekkonidae, *Gekko gecko*). 2) Geography (e.g. China, Thailand). 3) Subject (e.g. taxonomic validity, ecology, biogeography). The order of taxonomy, geography, and subject should be observed.

Text

Manuscripts must be in English and spelling must be correct and consistent. Use *Webster's New International Dictionary* for reference. For clarity, use active voice whenever possible. For example, the following sentences in active voice are preferable to those in passive voice.

Active voice: "Lizards were extremely common on the site." and "I examined three female snakes."

Passive voice: "Lizards were observed to be extremely common on the site." and "Three female snakes were examined."

Abbreviation

Do not abbreviate unless the full phrase has already appeared. Scientific names may be abbreviated only if they have appeared fully in the same paragraph. Never begin a sentence with an abbreviation of a scientific name.

Statistics

Statistics must be accompanied by sample sizes, significance levels, and the names of any tests. Investigators should pay careful attention to independence and applicability of tests, and randomness of samples. One of the most frequent examples of nonindependence is the use of multiple, paired t-tests instead of analysis of variance (anova). In general, multiple tests on the same data set are not valid. Descriptive statistics are in many cases more appropriate than inferential statistics.

Standard Format

Manuscripts following standard format should include introduction, methods, results, and discussion sections. While other formats are acceptable, the editors encourage the use of standard format. **Please do not type in all capital letters**.

Introduction

The introduction typically states the significance of the topic and reviews prior research.

Material and Methods

This section should clearly state where, when, and how research was carried out. Include sample sizes. Protocols designed by other investigators must be properly cited. Research materials and their manufacturers should be listed. The reader must be able to replicate the methods of the author(s).

Results

This section states the results and their significance to the investigation. Figures and tables may be used to clarify, but not to replace, results statements in the text. Statistics should be used when applicable. Large amounts of data should be avoided, or included as an appendix at the end of the article.

Discussion

The discussion is a synthesis of the introduction and the results. No new information should be discussed unless it was presented in the results section. New findings should be discussed in relation to prior research. The author(s) should feel free to present several possible interpretations of the results. The editors particularly encourage suggestions of future research in Asian herpetology.

Manuscript Preparation

Overview

Please do not attempt to replicate the formatting style of AHR in your manuscript. All formatting except italics will be removed in the production process. Bold and underlined text should be used only to identify section heading levels (see below). Extraneous formatting is counterproductive and increases the production costs of the journal. There are a few simple guidelines that authors must follow.

Section Headings

Articles will be published using three section heading styles. All heading levels must be on their own line, and left justified. For the purposes of manuscript submission, Level 1 heading is **bold**, and generally reserved for Introduction, Material and Methods, Results, and Discussion; Level 2 is *italic*, and Level 3 is underlined.

Figures

Figures **must** be referenced in order in the text. Each figure illustration (line art or photograph) submitted must be "camera ready" for publication with no modifications necessary other than reduction. AHR does not publish "plates"; please refer to these as figures numbered sequentially. Do not write on figure; do not mount more than one figure to a sheet. AHR cannot be responsible for redrawing, touching up, or otherwise modifying figure illustrations for authors. In addition, figure illustrations submitted must:

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2) be mounted on a separate 21.5 x 28 cm (8.5 x 11 inch) sheet with figure number on back.

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Figure Legends. Figure legends should be typed on a separate sheet. Legends should explain the figure without reference to the text. A figure and legend should make sense if separated from the rest of the article. For example:

> Figure 2. Lateral view of live *Psammodynastes pulverulentus* holding a prey lizard (*Anolis carolinensis*). Note buccal tissue surrounding the enlarged anterior maxillary and dentary teeth of the snake.

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Tables

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Typeface

Twelve point type is preferred. Supply a detailed list of special characters (greek letters, male or female symbols, etc.) that are not part of a standard font.

Literature Cited

Accurate and standard references are a crucial part of any article. This is especially important when dealing with publications from many different countries. The reader must be able to precisely identify any literature cited. References in the text must be checked for consistency with references in the literature cited section. All references cited in the text must be in the literature cited section. The literature cited section may not contain any references not mentioned in the text. Articles containing inaccurate or inconsistent literature citations will be returned for correction.

References in Text. 1) References to articles by one or two authors must include both surnames in the order they appear in the original publication. References to articles by more than two authors must include the first author's surname, followed by "et al." 2) The year of article follows the authors, separated only by a space. 3) References with the same author and year are distinguished by the lower case characters "a, b, c, . . ." 4) References cited in text are listed in alphabetical order by first author.

For example, "My results also incorporate literature records (Marx et al., 1982; Marx and Rabb, 1972; Mertens, 1930; Pope, 1929; Wall, 1909, 1910a, 1910b, 1910c)."

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Journal article

Dial, B. E. 1987. Energetics and performance during nest emergence and the hatchling frenzy in loggerhead sea turtles (*Caretta caretta*). Herpetologica 43(3):307-315.

Journal article from a journal that uses year instead of volume

Gatten, R. E. Jr. 1974. Effect of nutritional state on the preferred body temperatures of turtles. Copeia 1974(4):912-917.

Journal article, title translated, article not in English

Ananjeva, N. B. 1986. [On the validity of *Megalochilus mystaceus* (Pallas, 1776)]. Proceedings of the Zoological Institute, Leningrad 157:4-13. (In Russian).

Note that for Acta Herpetologica Sinica, the year must precede the volume number. This is to distinguish between the old and new series, and between 1982-1987, Vols.1-6 (new series) and 1988 with no volume number, numbers 1 and 2 (new series).

Cai, M., J. Zhang, and D. Lin. 1985. [Preliminary observation on the embryonic development of *Hynobius chinensis* Guenther]. Acta Herpetologica Sinica 1985, 4(2):177-180. (In Chinese).

Book

Pratt, A. E. 1892. To the snows of Tibet through China. Longmans, Green, and Co., London. 268 pp.

Article in book

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Thesis or dissertation

Moody, S. 1980. Phylogenetic and historical biogeographical relationships of the genera in the Agamidae (Reptilia: Lacertilia). Ph.D. Thesis. University of Michigan. 373 pp.

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